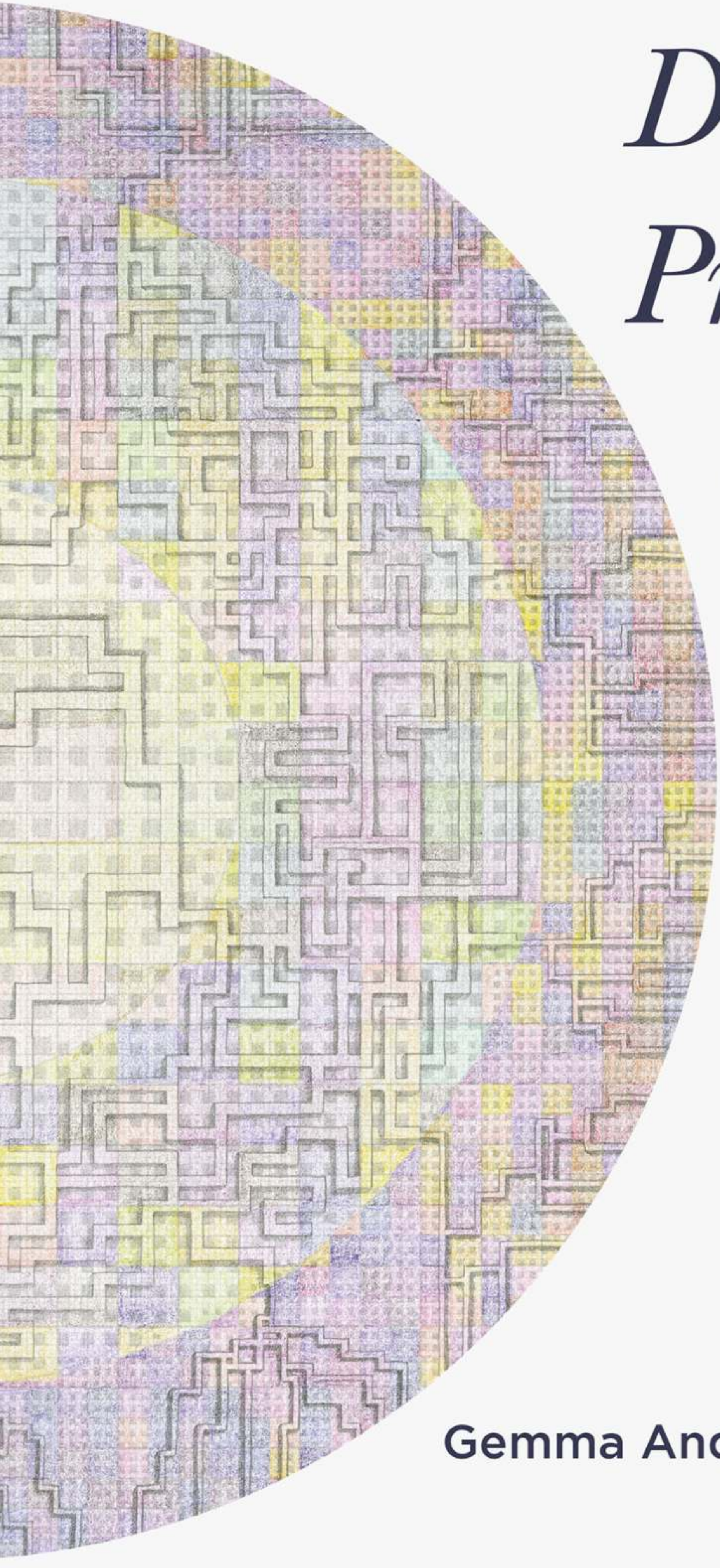

Drawing Processes of Life

Molecules, Cells, Organisms

Edited by
Gemma Anderson-Tempini
John Dupré

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Foreword: Symbiotic Perspectives on the Processes of Biology and Art

Scott F. Gilbert

This is a rather subversive book. It's a volume about science, art and freedom. It doesn't try to make bridges between art and biology because it finds no such separate entities or processes to bridge. While the disciplinary field of biology may interact with the disciplinary field of art, biology and art don't interact. They interpenetrate each other. This perception leads to a startling and perhaps unsettling conclusion: changes in our knowledge of biology demand similar changes in how biology is represented. The new biology and the new representations of biology mutually reinforce one another. As biologist and historian Michel Morange (2011) noted, 'To introduce a new representation is an event that is as important in the construction of scientific knowledge as technological developments and the unveiling of new phenomena'.

New biologies coincide with new representations. Think of Darwin's 'tree of life' or the Watson and Crick 'double helix'. Each of these representations has become an icon of biology, found on logos, t-shirts and in our minds. Other examples include Maria Sibylla Merian's depiction of a life cycle, Jane Richardson's 'ribbon diagrams' for folded proteins, and C. H. Waddington's epigenetic landscape. These drawings did not change the data; they changed the way we perceived and organized the data. The illustrations suggested new sets of questions for scientists to ask. They gave artists new ways to draw and new ways to represent living beings.

So one should expect that as biology changes, the old bottles will not be able to contain it. Twenty-first-century biology is not like twentieth-century biology. Our present biology is not about entities such as genes or organisms; it is about relationships. Here, the gene isn't a gene until the DNA gets 'interpreted' as one by the nuclear proteins (Stotz et al. 2006; Stammatoyannopoulos 2012). The organism isn't an organism without the symbiotic interactions that develop and maintain its physiology. Twenty-first-century biology is not about stasis, but rather about processes (Nicolson and Dupré 2018). Indeed, just as physical objects can be represented as both particles and waves, living beings are both entities and processes. And these entities appear to be themselves concrescences of metabolic, developmental, and evolutionary processes (Gilbert 2017). There is an anagenic change occurring in biology, with systems biology, symbiosis, developmental plasticity and niche construction coming to the fore. What had been peripheral is moving towards the center. Complex networks of cooperation and competition between species and within an organism are becoming highlighted rather than simple competition.

Indeed, one of the most important changes presented by the new biology is the notion of organisms as 'holobionts'. A holobiont is a single individual composed of other individuals of many different species, and each plant and each animal can be considered a holobiont. About half the cells in the human body are symbiotic microbes, and they are integrated into our bodies' physiologies (Gilbert et al. 2012; McFall Ngai et al. 2013). We need these microbes to help mature and sustain our guts, capillaries and neurons. Moreover, the microbes and their hosts may be essential for the other. The holobiont cow, for instance, contains both the bovine cells derived from the fertilized cow egg as well as a set of microbes that it acquired from its maternal and pastoral environments. Amazingly, there is nothing in a cow's genome that enables it to eat grass. The digestion of plant materials is accomplished in the cow's stomach by her symbiotic microbes. The microbes, moreover, are allowed to propagate themselves within the gut of the cow. This is called mutual scaffolding (Chiu and Gilbert 2015, 2020). The microbes allow the existence of the cow; the cow perpetuates the existence of the microbes.

The holobiont is thus both an organism and a collection of ecosystems (Gilbert 2019; Suárez and Stencel 2020). This notion of bodies as holobionts may help solve a problem in visualizing the relationships between art and biology. We can represent art and biology as parts of a holobiont organism. Looking at it one way, art and biology make a single composite artscience organism. Looking at it another way, art and biology are different entities that can interact to form new types of structures. This dual *Gestalt* of foregrounding/backgrounding alternations between single and composite units characterizes physical biological bodies. It may also characterize bodies of knowledge.

Biologists and artists desperately need ways to represent such ideas and processes. How does one represent evolution when one thinks about evolution as changes in embryonic development over time? How does one represent organisms when they develop, flourish and evolve as consortia of mutually interacting symbionts rather than as monogenomic products of the fertilized egg? How does

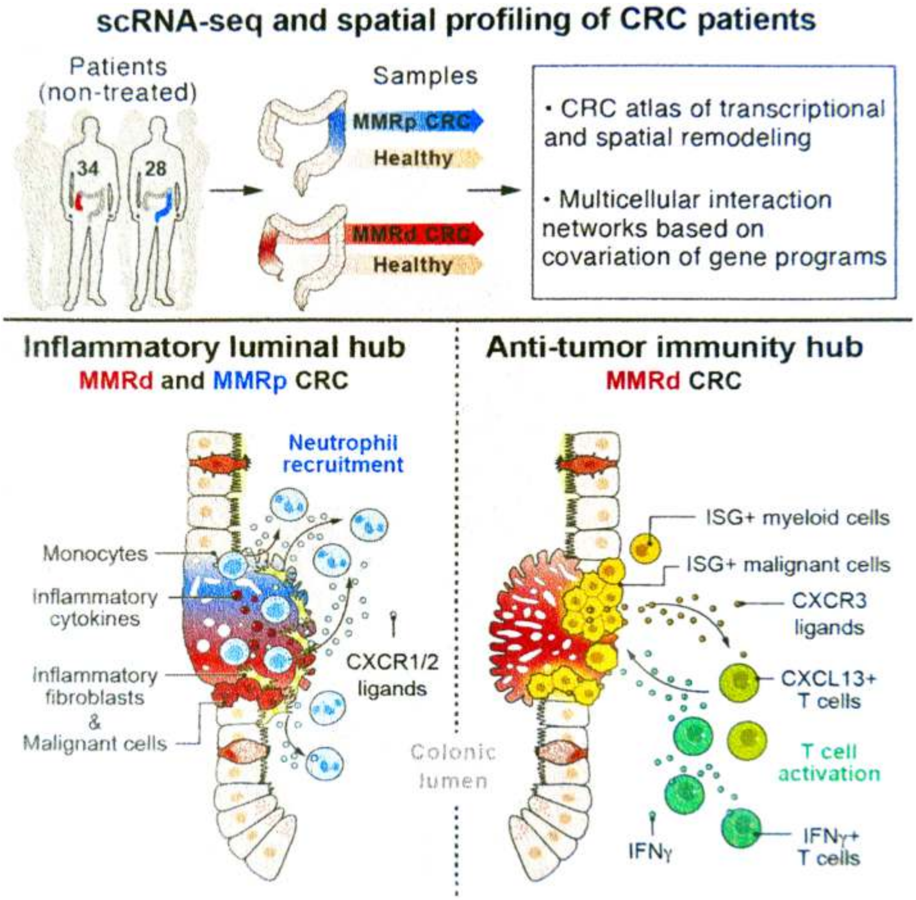

FIGURE F.1: Showing processes process in a 'Graphical Abstract'. This is from article 'Spatially organized multicellular immune hubs in human colorectal cancer', by Karin Pelka et al. (2021). It is from the journal *Cell*, which expects each article to be accompanied by such a graphical abstract. The upper panel represents the process of experimentation; the lower panels are interpretations of data, showing interactions in the gut between cell types in the production of inflammation (left) and anti-tumour immune cells (right), respectively.

one represent a life cycle that takes instructions from external living and abiotic sources? In short, how does one represent a biology of converging processes? How does one reconfigure one's laboratory, or one's studio, to study these new phenomena of investigation? Can two-dimensional imagery be revitalized in the era of animation and virtual reality? So this book is not, and cannot, be solely about how new art can represent and help generate a better science. It is also about the reciprocal processes whereby new science can promote new types of art and art practices.

The ability to use computers for visualization has changed the way we view data, but not how we view biology. Microarray data, for instance, are often graphed as 'heat maps', wherein one can visualize changes in the expression of several genes as conditions change. This improves the readers ability to see patterns, but this merely puts colour onto data otherwise represented as '0, + or +++'. Similarly, cluster analysis is now being taken from the social sciences to group biological entities as similar or dissimilar according to mathematical algorithms set with particular thresholds. But this, too, does not escape the static paradigm. It excels at distinguishing 'types'. Moreover, these types need not be 'real', but those that best fit the paradigm that informs the algorithm (Rosenberg et al. 2005; Yoder 2014). But biology has become a science of processes, and we are frustrated by our inability to represent these processes on paper.

Biological journals have realized this moment. Many of the most highly cited journals in the field now require 'Graphical Abstracts', and such abstracts are being required by an increasing numbers of journals over the past decade. Most of these Graphical Abstracts represent processes – either the biological process being delineated or the experimental process through which these new processes were found – and sometimes both, as in Figure F.1 (Hullman and Bach 2018). In these Graphical Abstracts, we can still see the power of drawings. In one sense, these drawings can be constricting. Graphical Abstracts provide a before-the-data channel for the mind to follow. The possibilities of the viewer's contribution is being narrowed. They are a biasing technique, marginalizing other interpretations. Note the multiple use of arrows in such a figure. These are the processes. It is in the arrows that the science occurs, and these processes are thereby hidden from the reader.

But these diagrams and drawings are not merely a lesser form of scientific illustration (Abrahamsen et al 2018). The Graphic Abstracts are different than illustrations, for they can more readily generate thought concepts. They can become carrier bags in which new ideas can be put together, jumbled up and reoriented into new configurations. One has freedoms in a drawing that one doesn't have in a photograph or realistic illustration. And the role of the audience is different. The viewer is more a participant in a diagrammatic process than an observer of an illustration.

Also, this book is not the answer to how biologists can best represent processes and the world of becomings. Rather, it is an embryonic landmark *towards* representations that can capture movement – a temporal dimension – on a two-dimensional surface. It is part of the process. The book is the product of biologists, philosophers and artists working together to formulate new ways of representing our new approach to life. It is a mutualistic symbiosis, where identities are transformed, information and nutritive substances shared, and where new organisms emerge.

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Introduction

John Dupré and Gemma Anderson-Tempini

This book has developed out of a trans-disciplinary project involving an artist (Gemma Anderson-Tempini), a scientist (a cell biologist – James Wakefield) and a philosopher of biology (John Dupré). Our project 'Representing Biology as Process' developed as Anderson-Tempini and Dupré had been working together on *Drawing as a Way of Knowing in Art and Science* (Anderson 2017) and were gradually moving their discussions from questions of classification and resemblance in drawing objects to the problem of providing images of processes. This, in turn, grew out of Dupré's long-term project arguing that biology generally should be thought of as the study of processes rather than of things or, in traditional philosophical terminology, substances (Dupré and Nicholson 2018; Dupré 2012, 2020). Biological imagery both informs and is informed by the orthodox treatment of biological systems as things. Traditional two-dimensional representations of biological entities or activities almost inevitably present a snapshot of the dynamic reality and can easily encourage inappropriately static interpretations of the represented phenomena. The idea emerged of trying to develop ways of representing biological phenomena that better captured their dynamic nature. Anderson-Tempini's first attempt to address this problem was a series of images that she entitled 'Isomorphogenesis' (2014), using a set of forms that she had developed in her earlier isomorphology project and a partially randomized artistic process.

At about the same time, and in connection with Dupré's ERC-funded project, 'A Process Ontology for Contemporary Biology', he and Wakefield had discussed mitotic spindle formation as a paradigmatic cellular process. These two streams of work came together to motivate the application to the AHRC that eventually funded the present project, 'Representing Biology as Process'. This project had three major goals: first, to explore and develop ways of using drawing to better represent biological processes; second, to produce art that was both biologically illuminating and aesthetically valuable and third, to explore the value of drawing as an epistemic tool in scientific research.[1]

This differed from Anderson-Tempini's previous work in taking her inside the scientific lab, where she developed novel ways of integrating her drawing practice with the scientific research taking place therein. Specifically, this involved the creation of a new kind of practice, the 'Drawing Lab'. This will be described in detail in the following chapters, in which we document the impact the drawing labs had on the practice of the scientists involved and on the refinement and refocusing of some of their research questions. This project also took Anderson-Tempini's work to a wider range of scales, addressing living processes beyond the visible to some that occur at the micro and nanoscale, including embryogenesis, mitosis (cell division) and protein folding. On embryogenesis, she collaborated with Alessio Corti, at Imperial College, and on protein folding with Jonathan Philips, at Exeter.

While the book revolves around the collaboration between Anderson-Tempini, Wakefield and Dupré, the aim of the present book is not only to present this work and the results of Anderson-Tempini's collaborations with other scientific projects but also to locate this in a broader historical and contemporary perspective on the relations between art and science. To this end, we have interwoven the results of our project with the work of a number of leading scholars in the field. Many of these contributions also stress the problems presented by the processual nature of biological phenomena, a central focus of our own work. Though this is an open-ended set of topics that we could not aim to cover comprehensively, we do believe that the perspectives presented here constitute a powerfully integrated and vital set of themes.

Process biology

The question of whether we should think of the world as consisting of entities statically defined by essential properties (in philosophical jargon, 'substances'), or as processes that undergo constant change, is a fundamental metaphysical dichotomy, debated since the pre-Socratics. Since the rise of atomism in the seventeenth century, the substance view has dominated scientifically grounded philosophy, and partly for that reason process philosophy has tended to languish. Dupré (e.g. 2020) argues that living systems are always dynamic at multiple spatial and temporal scales. What we think of as biological things persisting over time do not persist merely through the continued possession of essential properties but as the result of the finely articulated interplay of multiple processes. If there is an essence to a biological 'thing', whether an organism, a cell or a molecule, it is the activity that maintains its integrity. Constant activity is the condition of its existence.

As good an illustration of this as any is provided by the multicellular organism (Nicholson 2018). There are three main reasons why an organism should be understood as a process rather than a thing. First, an organism is a *developmental* process. The same organism may be, at different times, an egg, a tadpole and a frog. What makes it true to say that these are the same organism is not anything that they have in common, considered at particular moments of their existence, but the causal connections between these developmental stages. They are part of the same temporally extended causal process. Second, an organism is a *metabolic* process. Its continued existence, as a complex structure far from thermodynamic equilibrium, is dependent on trillions of molecular-scale activities every second. It persists not by default but through activity. And third, it is a symbiotic process. All, or almost all, organisms depend on intimate symbiotic relations with very different organisms, for instance in the gut microbiome. Again activity, an interaction with symbionts, is a condition of persistence. Moreover, the extent of symbiosis makes it difficult to say where the organism begins and ends. Is the skin microbiome part of the organism or something covering it? There seems no unique principled answer to this question, a situation very problematic for a traditional substance, but of no concern for a process: processes constantly intertwine and intersect in ways that make it hard to find unique boundaries between one and the next.

Representing such processes requires representing more than three dimensions, and more even than four dimensions with the addition of time. The four-dimensional history of, say, a cell is maintained and directed by its embedding in many further processes, reflecting its continuous interaction with its cellular, molecular and physical environment. In this sense, we think of biological processes as multi-dimensional, and in the work described in this book, we looked for ways of representing the relationships between multiple such processes.

Drawing

Visual representation is essential to both the practice and the communication of science. A serious problem faced in the development of a fully processual biology is that most visual representation strongly suggests a realm of static things. For example, the representation of an organism will be of a particular developmental 'stage', typically the mature adult, which obscures the fact that this is a momentary temporal stage of the developmental process. Even where a representation of something as plainly dynamic as metabolism, for example, will include arrows representing time, the natural reading will be of transitions between a fixed array of things (e.g. instances of chemical kinds). Moreover, while visual images or 'visual explanations' (Tufte 1997) in science depend on a variety of graphic devices ranging from the use of video and photography to the use of computational graphic software, simulation and hand-drawing, these means of making images largely depend on mechanistic models for, or of, their objects, which are already intertwined with their methods of production.

Whereas drawing in the past played a central role in fields such as morphology and embryology, the rise of photographic and digital technologies and the growing emphasis on molecules as opposed to whole organisms have increasingly marginalized drawing practices. We believe, for several reasons, that drawing has the potential for exposing the processual nature of living systems that these automated image-producing methods lack. First, and central to the epistemic benefits that drawing conveys, it allows the researcher to decide which features to represent or emphasize, and which to minimize or ignore. Second, and perhaps even more important, drawing is itself a process. In the words of Patricia Cain,

> Drawing is an intimate occupation; it is by nature a First Person activity because of the direct connection between the individual and the marks s(he) makes. Its most fundamental characteristic is that it evolves as it progresses – it is a process.
>
> (Cain 2010: 265)

Much biological representation in biology is of course of dead things, killed, fixed, stained and processed in countless ways to produce something relatively static. But if a thing is living it is active, even if not much at the spatio-temporal scales at which it is being observed. Active engagement with a living process, as is realized by drawing – itself a process – provides insights into the biological activity that are not easily achieved through the use of automated technologies that need not engage the researcher's attention at any point but the final production of an image.

In line with the growing interest in process-centred understandings of biology, the work presented in this book addresses the need for novel image-making practices to provide more intuitively dynamic representations of living systems through innovative collaborations between art, biology and philosophy, and attempts to show that drawing is a technology that can address this need. Although, over the last 30 years, drawing has been in a state of decline in scientific practice (Anderson-Tempini 2014), recently, as part of 'a huge growing interest in interdisciplinary research' (Trescot 2016), work in a number of disciplines has argued for the epistemological value of drawing (Ainsworth et al. 2011; Hay et al. 2013; Tversky 2010; Anderson-Tempini 2017; Casey and Davies 2020). This project asks two fundamental questions: How can drawing techniques be developed to provide the most illuminating and informative representations of active biological processes? And how can these techniques be used as a means of helping to interpret, reflect and theorize the processes it aims to represent (i.e. what is their epistemological value)?

Taking inspiration from Waddington's landscape

We have referred to process philosophy as a movement in opposition to the dominant substance-based ontology. But a wider view should recognize that process biology is not new in the twenty-first century. In fact, a high point in process thinking in biology can be located in the first half of the twentieth century, centring on a group of theoretical biologists and philosophers strongly influenced by Alfred North Whitehead, the doyen of British process philosophy (Nicholson and Gawne 2015). Most influential among these was Conrad 'Hal' Waddington. Waddington was the first scientist to use the term 'epigenetics' to conceptualize the interaction between genetic and environmental factors in development, and introduced the idea of the epigenetic landscape as a metaphor for the possible trajectories of development; this concept, if in a slightly modified sense, is widely used in theoretical biology to this day. He is perhaps best known for the images he made in collaboration with artists of the epigenetic landscape as a complex topography down which a marble can roll. As the marble descends through the landscape it passes various decision points, and its fate becomes increasingly fully determined, in a process he referred to as 'canalization'. The image provides 'a visual depiction of a set of developmental choices that is faced by a cell in the embryo, expressing the way these relations shape and channel development over time' (Slack 2002: 893; see also Hall 1992: 119).

Waddington's diagrams have been used in many ways. While they are most often interpreted as referring to the development of a cell, there are other possible applications. The images, at any rate, lend themselves to representing a diverse set of processes sharing a few core features typical of a wide range of biological processes: a forking pathway in which a decision at each fork irreversibly constrains future choices, and a landscape itself subject to change over time. As well as cells, tissues and whole organisms, the image could in principle be applied to a macromolecule or even an evolving lineage.

Waddington, moreover, as befits a thoroughly process-oriented biologist, was well aware of the different time scales involved in biological processes, and the interactions between phenomena at these different time scales:

> These three time-elements in the biological picture differ in scale. On the largest scale is evolution; any living thing must be thought of as the product of a long line of ancestors and itself the potential ancestor of a line of descendants. On the medium scale an animal or plant must be thought of as something which has a life history. It is not enough to see that horse pulling a cart past the window as the good working horse that it is today; the picture must also include the minute fertilized egg, the embryo on its mother's womb, and the broken-down nag it will eventually

> become. Finally, on the shortest time-scale, a living thing keeps itself going only by a rapid turnover of energy or chemical change; it takes in and digests food, it breathes, and so on.
>
> (Waddington 1957: 200)

Our different but complementary perspectives brought us to reconsider and extend Waddington's 'epigenetic landscape' (Waddington 1939, 1940, 1957). Beyond visualizing the paths taken by organisms during their embryonic development, this iconic image has the ambition to reunify embryology with genetics and evolution by representing the complex genetic and environmental changes that affect the topography of the developmental landscape. In this book, a number of case studies create and extend versions of this representation. We highlight how the conceptual image of the epigenetic landscape not only works as a metaphor for developmental processes but for all homeorhetic[2] processes; for example protein folding (Chapter 7).

Through a series of practice-based interdisciplinary drawing studies, centred around the work of Anderson-Tempini and the Drawing Labs and with complementary contributions from various scholars in the humanities and life sciences, the book's aim is to present drawing as a pathway to a new dynamic representation of living processes at the molecular, cellular and organismal scale. Our case studies offer examples of adaptations of Waddington's landscape that stimulate visual thought and enable us to contemplate biological processes in new ways. The epigenetic/developmental/homeorhetic landscape we conceive is one of life unfolding over time. We are adapting and evolving Waddington's concept of the epigenetic landscape as a tool crafted at the intersection of art and science. To paraphrase Waddington, his artful representation helps to 'loosen the joints of the scientist's imagination', creating a space for the associative play required to introduce new concepts in theory formation (Waddington 1968).

Philosophically, this work gives body to the idea that processes of art can resemble those of living organisms. A third process important for this book is that of scientific research.[3] An example of a novel way of carrying out scientific work is provided by the drawing labs described in Chapters 5 and 6. These are processes not only of artistic production but also, as we try to show, of scientific production. And of course, they are natural phenomena, the concerted behaviour of a group of organisms. As work in process biology has emphasized, the common fate of processes is to intertwine and thereby produce novel formations (Bapteste and Dupré 2013; Dupré and O'Malley 2009). In the present work, we show how artistic and scientific processes can intertwine and produce something new and illuminating for both the scientist and the artist.

Overview of chapters

Chapter 1, by K. Lee Chichester, takes us deeper into the connection between art and science in the work of Conrad Waddington. Chichester describes Waddington's deep and deeply informed engagement with the art of his time, and the ways in which art played an essential role in his scientific thinking, ending with an account of the thinking behind the iconic epigenetic landscape images co-created with John Piper. While Waddington is the central focus, Chichester also describes relevant ideas from various contemporary scientists, notably those involved with Waddington in the Cambridge Theoretical Biology Club. Especially important for chapters to follow is the insistence that art is not merely a representational tool for the scientists, but can profoundly inform scientific thought. As Chichester quotes Waddington,

> The scientist does not go to the painter for a representation of scientific objects, but for the enrichment and deepening of his consciousness, which comes when he finds a painter in whom the climate of scientific thought has penetrated into the spirit, leading to the production of works in which some of the deeper, less easily expressible, features of the scientific outlook are 'shown forth'.
>
> (Waddington 1969: 153)

In Chapter 3, Anderson-Tempini, Verd and Jaeger explore further possible developments of Waddington diagrams. The chapter provides a paradigmatic illustration of the use of dialogue between artist and scientist, mediated by the co-production of artistic images, for theoretical biological thinking. Starting again with Waddington's famous images, the authors attempt to develop novel ways of extending these to represent various oscillatory and other complex dynamics, in the process producing a remarkable series of images. The authors also reflect on the nature of this collaborative image-making and its implications for understanding the epistemic potential of drawing. The collaboration sheds light on both artistic and scientific methodologies for gaining insight into biological processes.

'Drawing as a pragmatist visual epistemology', Chapter 2 by Chiara Ambrosio, brings a further focus on one of the central themes of this volume, that drawing is a means of finding out, or knowing, and is an especially valuable epistemic tool in the context of a processual ontology. Drawing has great potential as a part of a process epistemology. Ambrosio frames this epistemic role in relation to the pragmatist philosophy that flourished in the United States from the late nineteenth century. She takes as her starting point the work of Charles Sanders Pierce, and his concept of inquiry as a fallible process of knowledge-seeking, which should take us from a state of doubt to a state of temporarily settled belief. Ambrosio proposes three ways in which drawing can be framed as a kind of visual inquiry and hence as a pragmatist visual epistemology: delineating, reconfiguring and structuring. Each of these three possible 'visual modes' of inquiry is illustrated and supported by case studies of drawing in action, in a concrete scientific context. This provides an exceptionally promising framework in which to think of drawing, in collaboration with laboratory science, as a mode of empirical investigation.

The next three chapters describe extended collaborations between Anderson-Tempini and scientists, and the development of the drawing laboratory. First, Chapter 4 derives from Anderson-Tempini's longstanding collaboration with mathematician Alessio Corti and explores ways of drawing the developing embryo. Starting from the 'Origami Embryo', developed as an educational tool by biologist Kathryn Tosney, Anderson-Tempini and Corti draw on methods developed in earlier work to translate Tosney's three-dimensional model into two-dimensional images of the embryo as a 'space–time worm'. In later sections of the chapter, Anderson-Tempini describes ways in which she has applied artistic license to develop these images beyond the confines of the scientific starting point. She relates this work to pioneering artistic experimentation by Paul Klee and to Goethe's 'Primal Plant'.

Chapter 5 then describes Anderson-Tempini's collaboration with cell biologist James Wakefield, exploring ways of drawing cell division, a major component of the AHRC-funded project involving Anderson-Tempini, Wakefield and John Dupré. This collaboration pioneered the Drawing Labs mentioned earlier. The chapter documents the development of these labs, and the eventual emergence of the idea of a mitosis score, in loose analogy with a musical score. Like a musical score, a canonical set of actions is ordered in a given sequence, but a good deal of latitude may be allowed in the details of this progression. Differences in the score were also deployed to represent mitosis in different classes of organisms and diseased cells. As in earlier chapters, there is a strong emphasis on the ways in which drawing is not just a technology for producing images of nature, but a method for generating hypotheses and concepts for exploring nature.

Chapter 6 moves to the molecular scale and describes Anderson-Tempini's work on protein dynamics with protein biophysicist Jonathan (J. J.) Philips, in particular addressing the complex process of protein folding, the trajectory from a sequence of amino acids to a mature three dimensionally structured protein. The chapter continues to develop the themes of drawing as a method of scientific exploration and, more generally, the possibility of a processual epistemology (Dupré and Leonelli 2022). The chapter also describes a series of drawing labs in which similar themes emerged to those from Chapter 4. The maze emerged as a new template, which allowed the presentation of such key features as fluidity, multiple interconnections and layering of processes. It is suggested that the maze might prove to be a template adaptable for drawing processes across the range of spatio-temporal scales (i.e. from two dimensions to multiple/higher number/order dimensions).

We have noted earlier the advantages of drawing over the automated production of moving images, as a way of engaging with and understanding the nature of a biological process. We did not mean to imply, however, that there is no place for the moving image of living phenomena, as Heather Barnett beautifully illustrates in Chapter 7 with her description of her film-making of the social amoeba, *Physarum polycephalum*. Her explicit aim is to explore and present the *Umwelt* (von Uexküll 1957) of this very alien organism, a collection of cells with nothing resembling a nervous system, but nonetheless capable of strikingly intelligent coordinated behaviour in response to various constructed environments. Of particular note in the present context is Barnett's discussion of the very different time scales experienced by different organisms and the challenges involved in translating the time scale of *Physarum* into a time scale meaningful to the human observer.

In Chapter 8, Wahida Khandker offers some fascinating reflections on the mimetic capacities of animals and relates these to aspects of Anderson-Tempini's drawing practices described in earlier chapters. She focuses especially on the extraordinary abilities of cephalopods to form coloured patterns on their skins with more or less clear mimetic functions. The most dynamic and least well-understood cephalopod displays – 'passing clouds' and 'flamboyant display' – suggest a 'sensory-expressive morphospace', parallel in tantalizing ways to the process of image production in Anderson-Tempini's isomorphogenesis, and in the expansion of isomorphogenesis described in Chapter 4. This, Khandker observes, is a kind of mimicry but, picking up a theme that recurs in this volume, 'one that is able to generate discussion rather than to delimit or to conclude it'.

Janina Wellman next addresses insect metamorphosis, one of the most paradigmatic cases of biological dynamicity, in Chapter 9. Using three beautiful historical case studies, she shows a transition from the pure preformationism of Jan Swammerdam (1637–80) to the genuinely epigenetic view of Johann Moritz David Herold (1790–1862). In each case, she shows how techniques of image production were integral both to the thought processes of the scientist trying to understand metamorphosis and to their ability to convey this understanding. This culminates with Herold's novel use of a sequence of gradually diverging pictures necessary to show the production in metamorphosis of something entirely novel. Wellman's overarching thesis is that the history of the scientific study of insect metamorphosis cannot be written without taking account of the visual representation of metamorphosis.

In a rather different vein, James Wakefield offers some more personal reflections on the experience of practising cell biology in a process-oriented way in Chapter 10. He contrasts this with the product-oriented approach that is more commonly assumed in contemporary science, in which what matters is just the accumulation of facts, theories or technologies. Wakefield notes, however, that there is also a strong drive to engage with the object of study that is lost in this approach, especially so when, as is less commonly the case with biology at the organismic or ecological level, the scientist is always separated from the object by an intermediating instrument, the microscope. Wakefield articulates in detail a way of doing biology at the microscopic level that attempts to achieve a strong connection with the material and suggests that an investigative process such as this is essential for taking seriously the processual nature of the subject matter.

Finally, in a concluding afterword, Sarah Gilbert and Scott Gilbert draw on a wide range of historical and contemporary sources to trace themes in the preceding chapters and draw out cross-cutting ideas about the natural world and our theoretical and visual conceptions of it. As perspectives on art and science interweave through this chapter around a range of core biological phenomena, they demonstrate as well as describe the interweaving of processes, scientific, artistic and non-human that the abstractive techniques of modern science so readily obscure. ‘Artscience’, they suggest, can help the scientists feel the interconnectedness between organism and environment that they already know; ‘it can help us slow down, feel, and even care’. If this book helps the reader slow down, feel, think and care, it will have achieved all that we hoped for.

NOTES

1. In this last respect, it also continues earlier work by Anderson-Tempini (2017) on drawing as a way of knowing.
2. A term used by Waddington, in contrast with the more familiar ‘homeostatic’, to refer to a process with a stabilized trajectory.
3. For further exploration of the implications of seeing scientific research as a process, see Dupré and Leonelli 2022.

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1

Conrad H. Waddington and the Image of Process Biology

K. Lee Chichester

In 1969, the Edinburgh Professor of Animal Genetics and pioneer of epigenetics, Conrad H. Waddington (1905–75), published a book under the title *Behind Appearance*, advertised as 'A study of the relations between painting and the natural sciences in this century' – a rather surprising topic for a renowned biologist.[1] Leafing through the heavy, hard-back catalogue reveals a richly illustrated, comprehensive analysis of the reverberations in modern art of the then recent 'Second Scientific Revolution' as marked by quantum physics, the principle of uncertainty and relativity theory. A book review preserved in Waddington's papers and penned by the German art historian and Harvard Psychology of Art Professor, Rudolf Arnheim, contains the scribbled note: 'I enjoyed doing this. Hope you are having a good year'. Arnheim, who may have met Waddington during his time in British exile, was visibly impressed by the breadth of the biologist's knowledge of the arts and the depth of his insight. 'He knows the arts from the inside', Arnheim remarks and conjectures that 'one would have to search a while to find so sane a guide among professional art critics'.[2] He distils as Waddington's central argument the observation that both the arts and the sciences had departed from external appearance in the first half of the twentieth century to penetrate behind the surface of things, into the energetic existence of matter in space–time. In doing so, they came to very similar results in visual and conceptual terms, as represented by abstraction in art and by formulas, models and instrumented visualisations in so-called 'Third Science'. The author, Arnheim concludes, does not interpret this as an influence of scientific images on the arts so much as the manifestation of a common worldview uniting both fields. What is astonishing, however, is that Arnheim, despite having published a study on *Visual Thinking* in the same year, does not mention the most striking aspect of Waddington's acclaim of contemporary art: namely, art's epistemic value to science. Beyond producing works that resemble scientific images, painters, according to Waddington, create sensual experiences by means of aesthetic experiments that aid in the discovery of new patterns in nature and help scientists grasp the meaning of their own theories and findings more deeply. Waddington thus went beyond most contemporary theorists of the relationship between art and science, who saw parallels mainly in the creative impetus and the aesthetic output of both fields.[3]

During the 1930s–40s, Waddington was part of a group of scientists and philosophers involved with embryology who tried to develop an understanding of the organism as fundamentally defined by process and organic wholeness. The post-Newtonian paradigm had introduced electromagnetic forces acting at a distance and hierarchical levels of complexity into physical science, making it possible for biology to claim laws specific to organic (and hence organised) systems. Suddenly, alternatives to mechanist explanation became conceivable that acknowledged wholeness without succumbing to vitalism. This however involved developing new images and models beyond what had so far been commonplace in biology. Art, as a field accustomed to concepts of wholeness, incremental complexity and organisation, became of interest to these biologists as a source of new models and ways of seeing the world. Most strikingly, as these scientists came to realise, the arts of the early twentieth century had already developed means of expressing dynamics, tensions and forces in static forms – in dialogue with gestalt psychology. It thus was no coincidence, as shall be argued in the following, that Waddington, like his collaborators Joseph Needham and John Desmond Bernal, looked to contemporary arts for inspiration and collaboration. Traces of this exchange can be found in the images of the ‘Epigenetic Landscape’ as developed by Waddington between 1940 and 1957, which emerged out of his work with Needham on the so-called ‘organiser’ and the meetings of the Theoretical Biology Club during the 1930s, as well as through his friendship with the Hampstead circle of British Constructivists and émigré artists.

A new biology required new images – much as in the ‘Representing Biology as Process’ project. In fact, as Thomas S. Kuhn’s concept of the paradigm suggests, the one does not seem to be possible without the other.[4] While the collaborations of the 1930s and 1940s were marked by friendships, studio and gallery visits, as well as perhaps a one-on-one workshop between Waddington and the artist John Piper, the current project has taken art as an explorative strategy in scientific research one step further: Gemma Anderson-Tempini, James Wakefield and J. J. Philips have intensified the art–science exchange through ‘drawing labs’, in which the scientists and the artist explore the possibilities of visual representation collaboratively. In both cases, the artists’ knowledge of spatial depiction, modeling materials and the construction of complex forms has opened up new ways of thinking about a reality that is not immediately accessible to human perception. Conceptualising the organism as process requires the creation of images indicative of dynamism, as well as the development of scores that allow for an analysis of time-based changes. In 1951, Waddington conjectured that

> [w]hen, or if, cinema becomes the most important technique of artistic creation, and movement one of the fundamental raw materials out of which beauty is created, then, perhaps, we shall have to turn our attention to the aesthetic characteristics of the developmental processes.[5]
>
> (Waddington 1951: 44)

Although new methods of registering living cells filmically have indeed redirected attention to process, the human mind continues to require static images for a deeper understanding of development.[6] In the 1930s, inspiration was found not only in drawings and paintings but also in abstract sculpture. This coincided with art critics' conceptualisation of modern artworks as organisms unfolding in time, responding to internal and external forces, which they made visible. The current essay hence looks back in time to create bridges to the present, relating one landscape to the other by arguing that it is no coincidence that biology in the organicist tradition once again engages in a dialogue with art.

How did artists enhance the representation of process and 'organism' in a manner productive for early organicist biology? Waddington's study *Behind Appearance* in fact begins with rather mainstream observations regarding the Impressionists' detachment of visual sense-perception from individual objects and the Cubists' integration of the fourth dimension into art (Waddington 1969: 9–31). Both styles had been brought into relation with post-Newtonian physics by prior commentators as well as by the artists themselves since the 1920s.[7] Waddington however argues that this revolution in art was equally relevant to science. In his eyes, a sufficiently complex synthesis of all aspects of the new worldview was achieved only by post-war Abstract Expressionism. He singles out its 'all-overness' as a main characteristic reflecting the fundamental outlook of 'Third Science' (Waddington 1969: 161). While the sciences and arts of the past had outlined a world made up of distinct objects, as confirmed by everyday experience, this concept, so intuitive to the human mind, had been replaced in modern physics by an endless and continuous energetic field perpetually in flux. This 'recognition that everything is involved in everything else, that the world is not an assemblage of isolated and detachable items but is a continuum of interlocking and mutually dependent activities', Waddington suggests, is not dissimilar to the impression conveyed by the paintings of Willem de Kooning or

Jackson Pollock (see Figure 6.1, p. 164) (Waddington 1969: 10). Their forms 'usually appear as though in violent motion, colliding and interpenetrating with a powerful sense of muscular or even inorganic energy' (Waddington 1969: 133–45, here p. 135). Instead of objects, we see trajectories of disembodied movement. It is this deeply and viscerally felt dynamism which, according to Waddington, marks Abstract Expressionism's value for the scientist groping for a deeper understanding of processual reality.

The fact that Waddington ascribes to the static traces of paint in de Kooning's and Pollock's paintings a kinetic energy points to his familiarity with gestalt psychology, presumably even with the work of Rudolf Arnheim himself. In an essay printed in the anthology *Aspects of Form*, published in the context of the *Growth and Form* exhibition at the Institute of Contemporary Arts in London in 1951, to which Waddington also contributed, Arnheim defines gestalt psychology as a science dealing 'with form only as the manifestation of forces, which are the true object of its interest'.[8] He further relates that:

> Only if one realises that all visual form is constantly endowed with striving and yielding, contraction and expansion, contrast and adaptation, attack and retreat, one can understand the elementary impact of a painting, statue, or building and its capacity to symbolise the action of life by means of physically motionless objects.
> (Arnheim 1951–61: 199)

Adopting his teacher Wolfgang Köhler's concept of 'physical gestalten', Arnheim attributes this sense of movement in static forms to the stimulation of electrochemical fields in the perceptual apparatus. Impressions of 'push and pull' evoked by a painting are hence interpreted as reflections of the organising forces of the central nervous system in its 'active struggle' to cope with incoming sense data. It is this 'struggle' that beholders subconsciously perceive as motion.[9] As Arnheim writes in an earlier article, 'the processes of organisation active in perception somehow do justice to the organisation outside in the physical world' (Arnheim 1943: 73.).[10] This isomorphic correspondence between the forces active in the physical world and in the physiology and psychology of perception ensures that physical laws become 'directly comprehensible to the onlooker' (Arnheim 1951–61: 208). These universal tendencies are also reflected in art, Arnheim claims, as artists attempt to balance masses and tensions between forms, creating dynamic equilibria that mirror the activity of their perceptual neural fields (Arnheim 1943: 74f.).

It is certain that Waddington knew Arnheim's writings at the latest by 1951.[11] Already in the early 1930s, he and his colleagues had dealt with the concepts of fields and physical gestalten in the context of their embryological work, which may have made him receptive to the art psychologist's writings.[12] And yet, Waddington's notion of a 'muscular energy' felt while beholding an action painting goes beyond this 'active struggle' of the perceptual apparatus. The idea may have been inspired by discussions with Ludwig Wittgenstein, whose after-dinner-walks with the psychologist Robert Thouless Waddington frequently joined at Cambridge in 1940–41.[13] Around this time, Wittgenstein was compiling his notes that were posthumously published as the *Philosophical Investigations*. In them, he sketched out a philosophy of language that ran counter to his early 'picture theory' of the *Tractatus Logico-philosophicus*. He now dealt with the more 'messy' aspects of language as a lived practice, for instance by comparing ambiguous words to bistable images. Considering the famous 'duck-rabbit', Wittgenstein suggestsed that when seeing the rabbit with its head turned to the right, beholders traced the image with their eyes, thereby reproducing its movement to the right: 'Look, how it is looking!' Wittgenstein writes, 'And at the same time, one looks accordingly' (Wittgenstein 2001: 1004).[14] There is a sense of bodily activation involved in viewing an image, Wittgenstein observes, a subliminal movement impulse – an effect he also ascribes to the understanding of words. For also the meaning of a word, felt spontaneously, must ultimately be an image or a bodily sense of movement. It seems that Wittgenstein was trying to make the concept of 'empathy', as developed by Robert Vischer, Theodor Lipps, Heirich Wölfflin and Vernon Lee around 1900, productive for the philosophy of language.[15] Already in 1931, the British art critic Herbert Read – who became good friends with Waddington in the mid-1930s – had cited Lipps in his book *The Meaning of Art*, explaining that:[16]

> When we feel sympathy for the afflicted, we re-enact in ourselves the feeling of others; when we contemplate a work of art, we project ourselves into the form of the work of art, and feel accordingly.
>
> (Read 1931–1936: 38)

Read maintained that we could 'feel ourselves into' any objects we observed, even abstract forms and simple lines: 'our physical sensibility must in some way be projected into the line – for, after all, the line itself does not move or dance; it is we who imagine ourselves dancing along its course' (Read 1931-36: 51). In Waddington's description of the effect of action painting on beholders, the trajectory of the marks on canvas is similarly felt as a muscular force, which he, in a second step, relates to 'inorganic energy'. The energetic existence of matter, which outstrips the human imagination, is thus felt, at least in an approximation, as a muscular activation, a subliminal impulse.[17] Only by means of such a sensory-motor perception can the iconoclastic, formulaic language of the New Physics, previously an empty envelope, be invested with meaning.

With this interpretation of Action Painting, Waddington offers a bold counter-narrative to the position of the influential art critic Harold Rosenberg. On the basis of Hans Namuth's photographic and filmic documentation of Jackson Pollock's painting process, Rosenberg had read Pollock's drip paintings as 'gestures' – traces of the muscular movements carried out by the artist in his 'dance' around the canvas.[18] To Rosenberg, they are no more than documents of individual moments in the artist's life, signs of his vital presence. The actual artwork is the action itself. Waddington decidedly rejects this viewpoint. None of the American post-war artists, he argues, ever understood their work as mere action. Instead, all had shown a keen interest in their paintings as material objects – as vehicles of expression and communication.[19] As the English art critic Lawrence Alloway had written in 1958, 'action was not the end result, but a process in the discovery of aesthetic order' (Waddington 1969: 138). The novelty of this aesthetic order, according to Waddington, was precisely its ability to suggest motion, process and energy, which it conveys as bodily sensation.

Waddington attributed the abstract expressionists' innovations in the ordering of visual space to their experiments with materiality and chance (Waddington 1969, esp. pp. 141–43 and 158–61). Pollock very deliberately determined which colours he employed where with which tools and in which amount. However, the ways in which the different oil- and water-based paints flowed over the canvas, how they chemically interacted and blended, lay beyond his control. Much like an organism, the painting, Pollock once said, 'has a life of its own' (Waddington 1969: 147, 165–69). This is impressively exemplified by the artist's drip painting *Number 1* (1948) depicted on a pasted-in colour plate in Waddington's book. Research carried out in the course of restoration work at the Museum of Modern Art in New York has shown that Pollock applied a first layer of paint to the canvas with his hands, leaving visible imprints in the upper right-hand corner (Figure 1.1).[20] On this very personal 'ground coat', he added a layer of brushwork and paint dragged directly from the tube, only then passing on to his famous, more haphazard drip technique. The painting documents a decisive shift in his medium, as he combined the impasto texture of oil paint with the more fluid flow of enamel and other industrial house paints. Oil- and water-based paints intermingle in pools on the surface of the canvas, creating marbled effects or drying in puckered patterns. In some paintings, Pollock turned the canvas up vertically in a final step to let the last layer of paint drip down through gravity. A close analysis thus vividly reveals the manifold ways in which the artist interacted with physical and chemical forces as well as with chance effects to produce a highly complex aesthetic order.[21]

Waddington accordingly characterises Action Painting as a participative process: in the production of a work, the artist collaborates with the qualities of materials and physical forces (Waddington 1969: 147). In doing so, a moment of indeterminacy remains. This is mirrored in the act of perception, since beholders can find almost anything in a drip painting that they bring to it in contemplation (Waddington 1969: 165, 169). From this, Waddington concludes that by dissolving the distinction

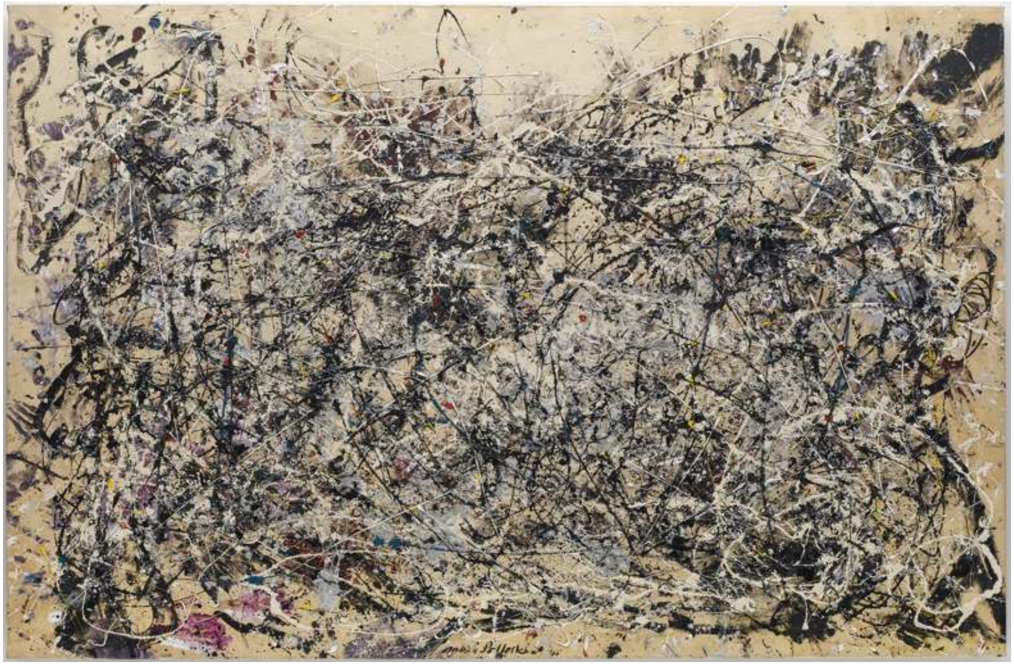


FIGURE 1.1: Jackson Pollock, *Number 1A*, 1948, oil and enamel on unprimed canvas, 172.7 × 264.2 cm. New York, Museum of Modern Art (MoMA). © 2022. Museum of Modern Art, New York/Scala, Florence.

between subject and object, the same revolution has taken place in painting that also marks 'Third Science': as Werner Heisenberg's Principle of Indeterminacy made irrevocably clear, scientists could no longer ignore the fact that they influence the objects of their investigation through their intervention. The footprint they find on the 'shores of the unknown', as Sir Arthur Eddington remarked, turns out to be their own – a fact seemingly reflected in Pollock's handprints (Waddington 1969: 108). Beyond acknowledging indeterminacy in measurement, Waddington recounts that more and more scientists had also begun to accept indeterminacy as a fundamental quality of the universe. Chance was not an artefact of yet undiscovered laws, but was reckoned to persist within the limits of natural law – a fact especially relevant to the more 'messy' sciences of life.[22] In analogy, Action Painting, to Waddington, represented a mixture of conscious human intervention, physical law and contingency.

Decisively, however, this style of painting made it possible, in Waddington's eyes, to affectively experience the new worldview. Regarding the paintings of Willem de Kooning he writes: 'De Kooning's paintings seem to me to be basically concerned with the way things interpenetrate one another, which he feels almost in terms of bodily sensation' (Waddington 1969: 138). Waddington relates this sense of 'feeling' to Alfred North Whitehead's concept of *feelings* and *prehensions*. Already as a philosophically attuned student at Cambridge, Waddington had read the works of Whitehead and discussed his philosophy in a paper on 'Philosophy and Biology', submitted for the prestigious Arnold Gerstenberg Prize in 1929.[23] In works such as *The Concept of Nature* (1920) and *Science and the Modern World* (1925), Whitehead had endeavoured to integrate the insights of quantum physics and relativity theory into a coherent philosophical outlook. Since everything was now conceived as standing in a structured relationship with everything else, he declared the *organism* to be the fundamental category of the physical world. Reality was made up of *events*, or 'slices' of the organism, connected in space and time. In result, every event, following Whitehead's terminology, has a *feeling* for other, related events – a condition he referred to as *prehension*, indicating a pre-stage of comprehension. It is no coincidence that Whitehead used concepts generally related to mental abilities in describing the physical world, as he attributed basic states of mind to inorganic nature. In Abstract Expressionism, Waddington not only recognised a sensual equivalence to this organised relatedness of various *events* in space–time but also evidence of the human ability to subconsciously *feel* or *apprehend* the structure of reality.

To Waddington, art is not of interest to science if it only echoes the images produced in the laboratory. It is of value only if it can enhance the scientists' consciousness. This happens when painting finds a manner of visualising those aspects of the physical world that cannot be expressed with words, or captured by modern imaging technologies:

> The scientist does not go to the painter for a representation of scientific objects, but for the enrichment and deepening of his consciousness, which comes when he finds a painter in whom the climate of scientific thought has penetrated into the spirit, leading to the production of works in which some of the deeper, less easily expressible, features of the scientific outlook are 'shown forth'.
>
> (Waddington 1969: 153)

The meaning of art, to Waddington, hence lies in its ability to create visual and bodily experiences that convey an intuitive understanding of phenomena in the physical world – while the mathematical language of science eludes true comprehension. As Albert Einstein once said in an interview with the mathematician Jacques Hadamard, which Waddington cites:

> The words of the language, as they are written or spoken, do not seem to play any role in my mechanism of thought. The psychical entities which seem to serve as elements in thought are certain signs and more or less clear images which can be 'voluntarily' reproduced and combined. The above-mentioned elements are, in my case, of visual and some of muscular type. Conventional words or other signs have

> to be sought for laboriously only in a second stage, when the mentioned associative play is sufficiently established and can be reproduced at will.[24]
>
> (Waddington 1969: 104)

In art, Waddington not only sees an effective means for internalising, and hence also popularising, the scientific worldview by empathetic absorption quasi ‘through the pores’ (Waddington 1969: 239). As the concept of visual thinking suggests, it can also be a medium of scientific discovery by instigating new ideas through unconventional aesthetic forms. Waddington compares Action Painting to Leonardo’s stained wall, declaring it as the best means for scientists to ‘loosen the joints’ of their psyche and ‘roll the bones’ of their ideas ‘to dredge up from the obscure internal depths something, which will probably not have the slightest obvious connection with the work of art […] – but which may be fresh enough to be worth while’ (Waddington (1969: 242). Art may thus help scientists find unexpected solutions to problems they are grappling with or come up with innovative models and concepts. As imagination, experience and feeling are all essential for the selection of relevant patterns in scientific research, Waddington concludes, ‘[a]rt and science are in true communication on the level of creativity’.[25] (Waddington 1969: 242).

Since it was Abstract Expressionism which, in Waddington’s eyes, first succeeded in finding an adequate visual form for the contingent and processual existence of objects as energies interacting in space–time, its development was also a major achievement for science. A painting such as Mark Rothko’s *Light Band* (1954) has a similar effect, Waddington writes, as Einstein’s famous formula E=MC^2, in so far as it brings the unfathomable complexity of the world, ‘which one can hardly think through in a lifetime’, into a most simple form (Waddington 1969: 172). It was not without reason that Rothko said of his work: ‘I am for the simple expression of complex thoughts’ (Waddington 1969: n.pag.). Endorsing the trained biologist and tachist painter Frank Avray Wilson, Waddington even goes so far to claim that, if scientists were to learn painterly techniques to represent their observations, they would have to be trained in Abstract Expressionism (Waddington 1969: 162f.).[26] This conviction that art can convey complex meaning through concrete material presence betrays Waddington’s familiarity with philosopher Ernst Cassirer’s concept of symbolic pregnancy (*symbolische Prägnanz*), as well as with Margaret Mead’s observation that ‘[m]an can […] learn by empathy, imitation, and identification; and he can transmit many types of meaning and feeling by incorporating them in something he has made, an artefact’.[26] (Waddington 1968: 72)

Not only Arnheim found Waddington’s familiarity with and understanding of the arts of his time impressive but also the art historian Ernst Gombrich sent Waddington a note from the Warburg Institute in London upon receiving his book, admitting: ‘I much admire & almost envy your close rapport with the artists of our time. I have never been so fortunate'.[27] Waddington was not only married to the architect Justin Blanco White; he was also friends with Henry Moore, Ben Nicholson, Barbara Hepworth, John Piper, Alexander Calder, Laszlo Moholy-Nagy, Naum Gabo and Walter Gropius, among others. Thus, the Hampstead artists so important in British Modernity belonged to his close circle of friends, next to influential émigrés from the Bauhaus and Constructivist movement. He was also in contact with a younger generation of artists, among them György Kepes, Richard Hamilton, Eduardo Paolozzi and Bridget Riley, and corresponded with international curators and art critics such as Herbert Bayer, Sigfried Giedion and Jasia Reichardt. As mentioned, one of the most influential British art critics, Herbert Read, was among his closer friends, and Read's biocentric art theory appears to have left a deep trace in Waddington's thinking about organicism and process in art.[28]

But what relevance did art have for Waddington's own research in Biology in the 1930s and 1940s? As a student of Paleontology, Waddington only came to biology in the late 1920s, presumably encouraged by his friend Gregory Bateson, son of the famous geneticist William Bateson. What seems to have drawn him to the life sciences was the promise of emerging molecular biology to bridge the gap between biology and physics by offering biochemical explanations for self-regulatory developmental processes in the organism. The age-old debate between mechanists, who likened the organism to a machine, and vitalists, who believed in an inexplicable life-principle – referred to by the German biologist Hans Driesch as 'Entelechy' – seemed to be on the brink of resolution. The integration of field forces, hierarchical levels of complexity and gestalt principles into the New Physics promised to make the wholeness of organisms explicable physically and chemically, without reverting to vitalist concepts of an intelligent, controlling life force.[29]

Waddington sought empirical training during a six-month appointment at Otto Mangold's laboratory for developmental biology (*Entwicklungsmechanik*) at the Kaiser-Wilhelm-Institute in Berlin-Dahlem in 1931. There he met the biochemists Joseph and Dorothy Needham, who, like him, had travelled to Berlin from Cambridge to become acquainted with work on the so-called 'organiser', pioneered by Mangold's doctoral supervisor, Hans Spemann, and his late wife, Hilde Mangold. Spemann and Hilde Mangold had introduced the term 'organiser' to refer to a group of cells in the embryonic tissue of amphibia that seemed to regulate cell differentiation in early stages of development. What remained to be determined was the identity of the chemicals ('evocator') which controlled pattern production in the embryo and the mechanisms by which these morphogenes were able to act in an organised way. Back in Cambridge, Waddington and the Needhams joined forces to continue their 'organiser work'. They eventually came to the conclusion that not so much an individual substance is decisive for developmental activation and organisation, but rather chemical or electromagnetic balances and gradients. This supported their systemic approach, which prioritised the interaction of manifold processes and influences over individual causes.[30]

The group tried to spell out the theoretical implications of their organicist approach in the context of the so-called Biotheoretical Gatherings held about once a year between 1932 and 1938.[31] Next to invited guests, further core members included the philosopher of science Joseph H. Woodger, the crystallographer John Desmond Bernal, and the mathematician Dorothy Wrinch. The aim of their meetings, which later became known as the Theoretical Biology Club, was the philosophical founding of a 'Third Way' in biology, distinct from both mechanism and vitalism. The idea that the whole is something different from the parts and that the parts determine the whole as much as the whole determines the parts, which they adopted from gestalt psychology, became a guiding concept, next to principles from emerging systems theory. They thus found it possible to claim independent laws for biology without leaving scientific ground and surrendering to vitalist metaphysics.

To the members of the Theoretical Biology Club, organicism was more than a scientific concept; it was also a model for society. Their belief in the relevance of organicism as a next stage in the dialectical development of society was just as inspired by Marxist readings as their commitment to the popularisation of science and its utilisation for the benefit of all. The presentations of the Russian delegation at the 2nd Conference for the History of Science and Technology in London in 1931 had consolidated their belief in the importance of technological innovation for scientific progress.[32] This 'externalist' approach to the history of science, which holds that ways of thinking are fundamentally (in-)formed by ways of being – for instance the use of technologies and the body in everyday life – and that science is propelled by social and technical needs, was soon closely associated with what became known as 'Bernalism', following J. D. Bernal's prolific publications on planned science, foremost his *The Social Function of Science* (1939).[33] Informed by externalism, the group realised early on and explicitly addressed the problems of modeling and visualisation accompanying the transition from a mechanist to an organicist worldview. Since the Early Modern period, human thought had been trained by the use of mechanical instruments, which had become the model for nature, including biological systems.

In 1944, a radically interdisciplinary publication under the title *This Changing World* appeared, aimed to make the most recent scientific and cultural developments accessible to a broad readership, in an attempt to restore a sense of unity and trust in modernity that had been shaken by two world wars and the increasing specialisation of disciplines.[34] Next to an introduction by Herbert Read, the volume includes essays by Waddington, Needham and Bernal. Waddington in his text laments that humans had so far modeled themselves and the world in wrong pictures: ‘We can show, I think, that the difficulty of making an adequate mental picture of a human being was largely due to the fact that we tried to think in the wrong terms’ (Waddington 1944: 39).[35] Most people still imagined the world in terms of models originating in the seventeenth century, when mechanics was introduced as the new scientific paradigm: ‘We “instinctively” think of solid lumps of stuff, and if they happen to be pushing one another around in some process, that may be interesting but is not essential’ (Waddington 1944: 47). Finding a more adequate image would, however, require a certain effort of the imagination. It is time, Waddington urges, to learn to look at the world differently, under the recognition that the process is more important than the individual particles. In this regard, he maintains, art has pressed ahead in finding ways to represent dynamics and forces. Referring to art historian Hartley Ramsden’s essay in the same publication, Waddington asks:

> Would E. H. Ramsden allow me to suggest, I wonder, that the shifting of interest among painters from the material object to the underlying form – for instance, the painting of the *wind* in the trees rather than the trees themselves […], or the creation of mobile sculpture by artists like Calder – is another part of the same trend as the scientist’s movement away from analysing into things and towards analysing into processes?
>
> (Waddington 1944: 48)

While the mentioned artworks are not illustrated in Waddington’s essay, depictions of Alexander Calder’s mobiles as well as Naum Gabo’s early kinetic sculptures do appear in a catalogue published a few years earlier, to which Bernal had contributed an essay. *Circle: International Survey of Constructive Art* was edited by Nicholson, Gabo and the architect Leslie Martin in 1937, Barbara Hepworth being responsible for the layout. Hepworth was presumably also the one who invited Bernal, whom she had met through her close friend, the philosopher and patron of arts Margaret Gardiner, Bernal’s then-partner. The sculptor greatly relished the X-ray crystallographer’s visits to her studio, where they would discuss questions of geometry and crystallography, drawing diagrams on the studio floor. She especially valued his critique of her sculptures, as he knew the formulas underlying her forms as much as their geometrical shortcomings and would sometimes note a formula under her works as if they were mathematical models (Burstow 2014: 54).[36]

In his article, Bernal not only reminds readers of the driving force art had for science in the Early Modern period, when art and architecture gave rise to the sciences of accurate observation and mechanics. He also remarks that with respect to the kinetic effects of static forms – impressions of ‘dynamic balance in movement’ – artists had been solving problems for which the theoretical formulation was still wanted.[37] Moreover, he sees artists making similar discoveries in their formal experiments as mathematicians in complex geometry. Bernal shows himself deeply impressed by the 'extraordinary intuitive grasp' exhibited in Constructivist sculpture with regard to surfaces which, though separated by space, 'belong together both for the mathematician and the sculptor' (Bernal 1937: 120f.). He illustrates this by comparing Hepworth's sculpture *Two Forms* (1937) with a visualisation of the equipotential surface of two like charges in an electromagnetic field (Figure 1.2). Much like Hepworth's sculptures, which in their slightly ovoid shapes seem to stand in communication, the equal charges, by repelling each other, produce two slightly non-circular forms clearly interacting across space. With this example, Bernal demonstrates that the laws of the invisible and ephemeral physical world can be expressed in static, tangible artistic form.

This conviction may have been informed by art critic Herbert Read, who since the early 1930s had interpreted the Constructivism of artists like Gabo, Hepworth, Moore and Nicholson as a reflection of forces and processes active in all things organic, bringing about order, pattern and geometric form (Thistlewood 1984: 94f.).[38] He came to believe in an equivalence of these formative processes in art and nature, understanding both in a Whiteheadian sense as organic events unfolding in time (Thistlewood 1984: xiif, 94f.). This idea seems to have been supported by his discussions with Moore, who already in 1930 had stated that the sculptor's formal understanding comes 'from nature and the world around him, from which he learns such principles as balance, organic growth of life, attraction and repulsion, harmony and contrast' (Thistlewood 1984: S. 99). Read thus came to regard Moore's sculptures as 'biologically significant' as they expressed 'the forms which matter assumes under the operation of physical laws' – an interest reflecting both Moore's reading of D'Arcy W. Thompson's *On Growth and Form* (1917–42) as a student in Leeds in 1919 and Read's discovery of Thompson's book sometime before 1934.[39] This idea is neatly exemplified by a sculpture depicted in *Circle*, which Moore had carved out of wood (Figure 1.3). The rounded figure stands unstably on its plinth, leaning slightly backwards, as if in a frail balance. Its rounded surface, reminiscent of the end of a tibia, still holds the traces of Moore's chisel, while also indicating the process of its natural 'ontogenesis' through the growth rings. The sculpture expresses dynamism in its stereometric form as well as in its surface modulation, the lines of its structure flowing across the figure like waves.

Hepworth was another artist who adopted Thompson's theory of form as a 'diagram of forces' resulting from the interaction of matter with forces from within and without.[40] In contrast to the traditional practice of sculpture that Hepworth and Moore had learnt at the Leeds School of Art and the Royal Academy of Arts in London in the 1920s, both worked as carvers. Instead of making plaster maquettes to be transferred to stone in a second step (often by assistants), they searched for form directly

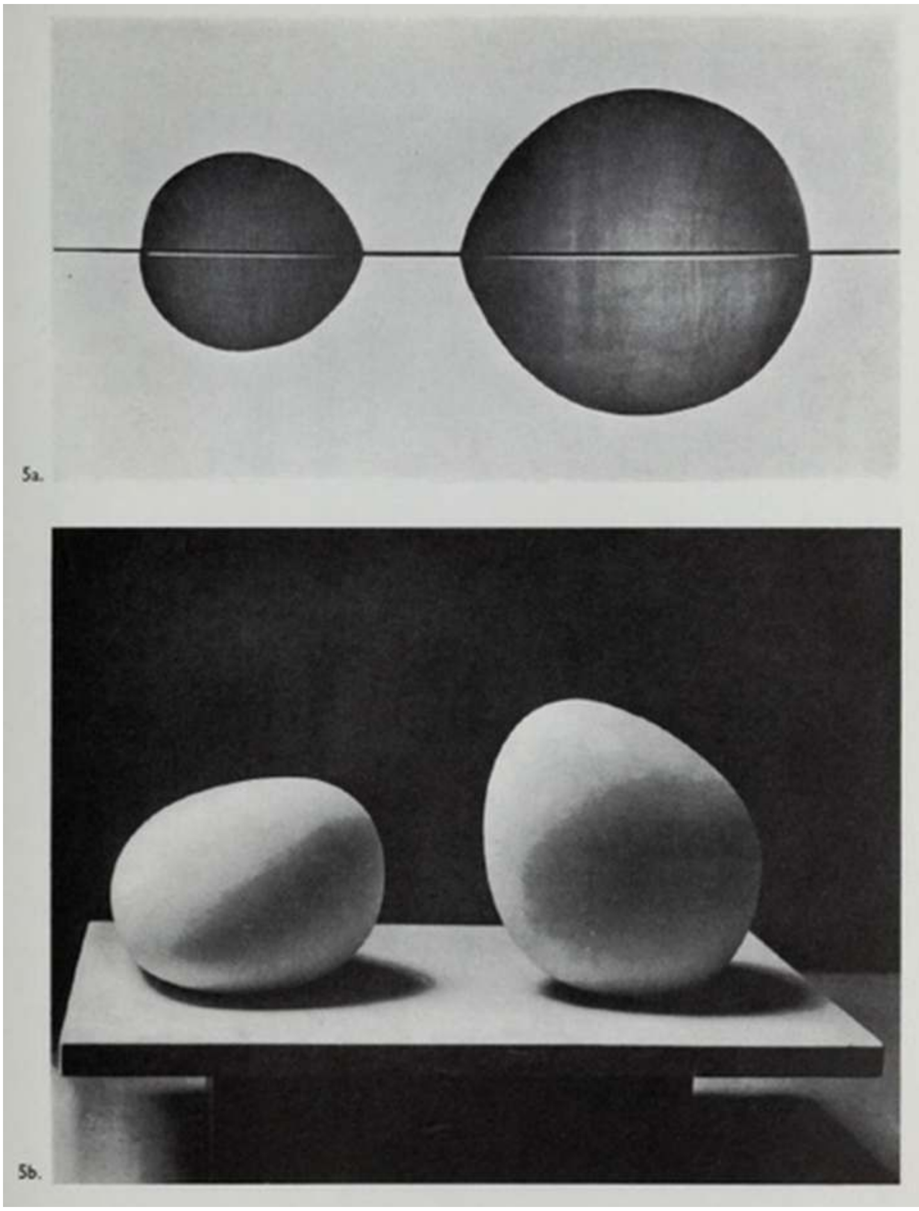


FIGURE 1.2: Illustrations in John Desmond Bernal's essay 'Art and the Scientist' showing two like charges and Barbara Hepworth's *Two Forms* (1937), in: Ben Nicholson, Naum Gabo and Leslie Martin (ed.), *Circle: International Survey of Constructive Art*, London: Faber&Faber, 1937. Copyright: Barbara Hepworth © Bowness.

within the natural material itself. The final form was not conceived of in advance but developed in the working process (Clayton 2021: 36, 41). As David Thistlewood has shown, Read eventually fleshed out a theory of organic art as the manifestation of dynamics of growth and development in the production of an artwork, which emerges

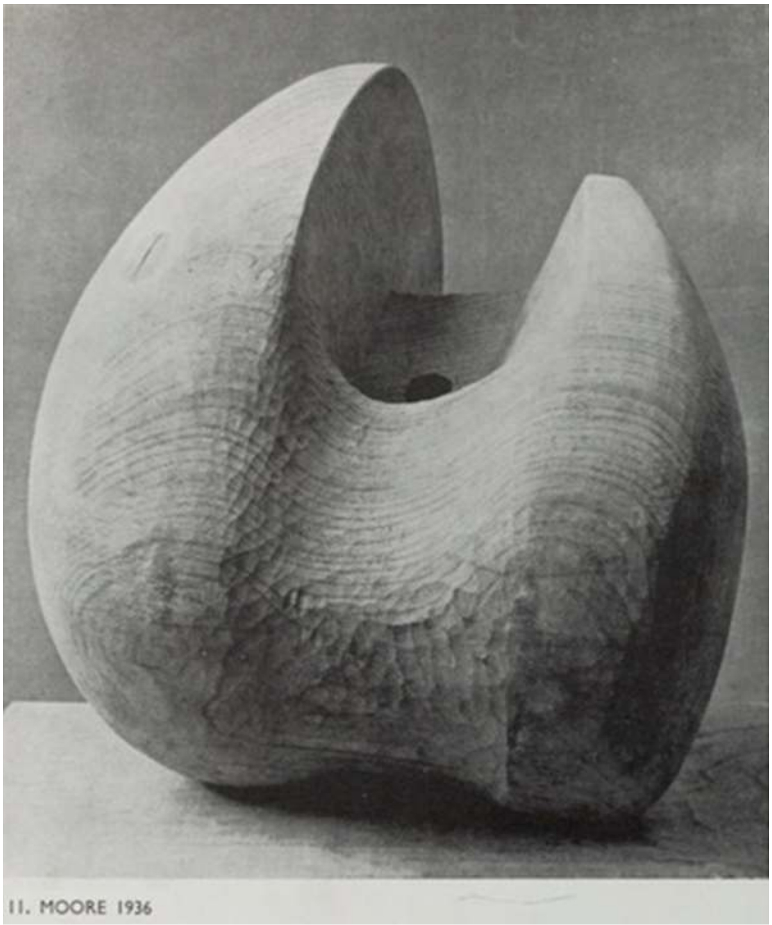


FIGURE 1.3: Sculpture by Henry Moore, 1936, in: Ben Nicholson, Naum Gabo and Leslie Martin (ed.), *Circle: International Survey of Constructive Art*, London: Faber&Faber, 1937. © Henry Moore Foundation.

through the interactions of matter and force in the intuitive, open-ended and time-based process of its creation (Thistlewood 1984: n.pag.). As Hepworth and Gabo made clear to Read, and perhaps also to Bernal and Waddington, they considered their abstract sculptures as deeply organic, expressing 'the basic forms of primary construction' essential to organic nature in its growth and development (in Thistlewood 1984: 86).[41] Read eventually came to see Hepworth's works as experiments with dynamic equilibria through continuous oppositions, which destroy static balance. In her own words, she explored 'the relationships in space, in size and texture and weight, as well as in the tensions between forms' (Clayton 2021: 72). It was not by coincidence then that Waddington assigned a leading place to British Constructivism in the development of images reflecting the organicist, process-based and relational perspective, identifying their work as 'one of the boldest of recent attempts to express visually a comprehensive natural-and-social philosophical synthesis' (Waddington 1969: 55). While previous geometricising developments had been 'either predominantly static, or, as with the Futurists, kinetic, with an emphasis on movement, but hardly at all dynamic', the British Constructivists placed an emphasis on force (Waddington 1969: 55).

In 1936, Hepworth, Moore and Nicholson were part of a travelling exhibition under the title *Abstract and Concrete* that was to present the new abstract art of Britain and Europe to larger audiences in Oxford, Liverpool, London and Cambridge (Figure 1.4). The members of the Theoretical Biology Club hence may well have seen the show at one of the latter two venues. Photographs from the exhibition as displayed at the Lefevre Gallery in London show Hepworth's *Two Segments and Sphere*, a radically geometric work, displayed adjacent to one of Nicholson's white reliefs and Mondrian's grid paintings. All three artists were interested in balancing acts of space and figure, line and colour, creating tensions between forms and impressions of dynamism. Displayed as a group, the works even seem to enter into relationships with one another, Hepworth's sculptural forms – with a sphere balancing precariously on top of stacked stereometric bodies – recurring in Nicholson's reliefs or acting against the background of Mondrian's grids. Like Hepworth, Mondrian understood his works to be microcosms reflecting universal laws in their balance of forces. As Waddington writes in *Behind Appearance*: 'Putting it in the broadest way,

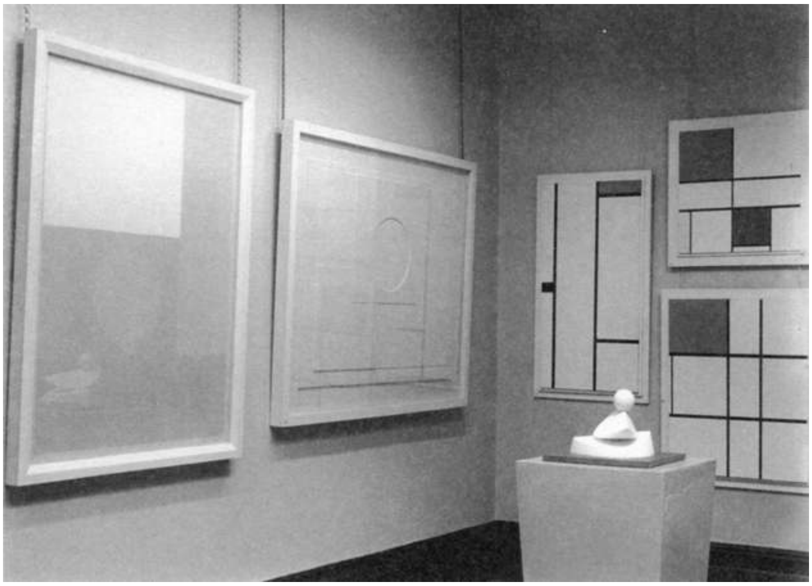
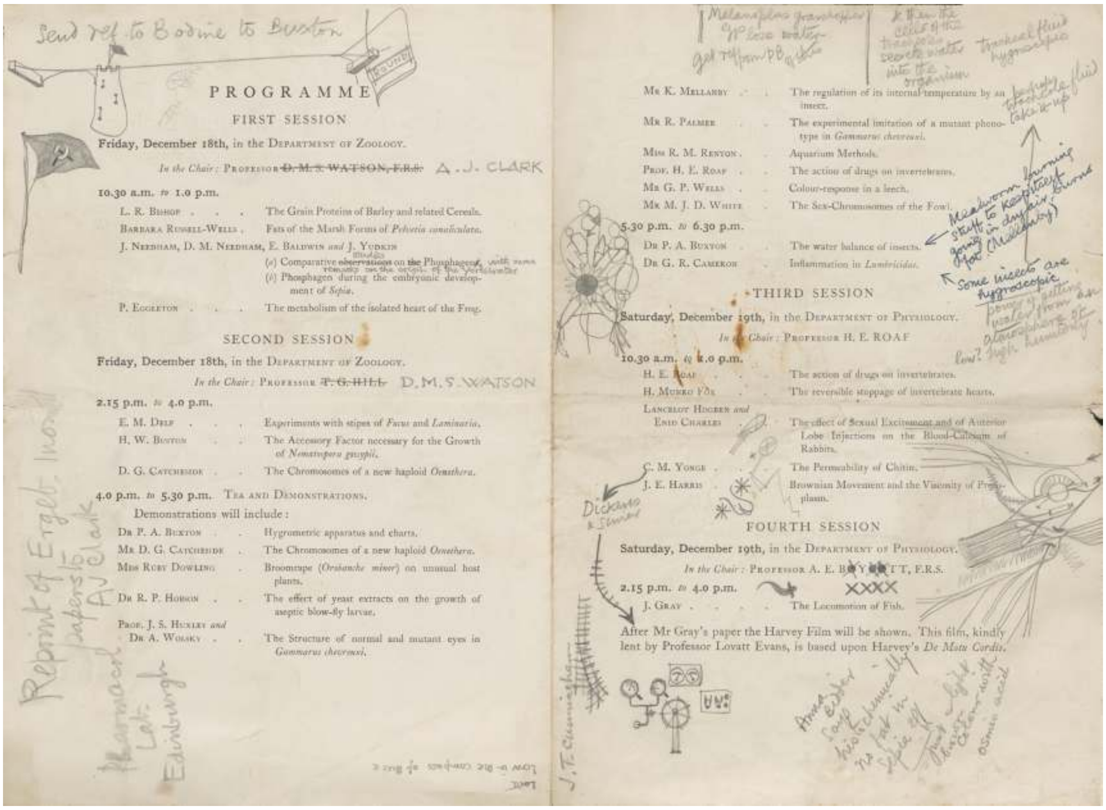


FIGURE 1.4: Exhibition view *Abstract & Concrete*, Lefevre Gallery, London, 1936. © Lefevre Gallery, London.

they saw the world in terms of equilibria which resolve tensions' (Waddington 1969: 55). Being exposed to such works in the mid-1930s seems to have left an imprint on the minds of the members of the Theoretical Biology Club that came to fruition in their work on embryogenesis.

Though Waddington retrospectively recognised the relevance of these artists' experiments with the dynamics of form to the search for new models of development in organicist biology, the representation of complex processes in embryogenesis – processes which were largely inaccessible to observation and involved various unidentified agents – presented a challenge at the time. The difficulties encountered become evident in sketches on Joseph Needham's conference program for the meeting of the Society for Experimental Biology in December 1931, shortly after his return from Berlin (Figure 1.5).[42] The conference flyer is strewn by notes and doodles revealing, next to his socialist sympathies, his obsession with rail systems. The drawings show rail lines branching out, a switchyard and a turning platform. The organisation chart in the middle of the double page even acquires an ornamental character with its floral



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PROGRAMME

FIRST SESSION

Friday, December 18th, in the Department of Zoology.

In the Chair: Professor ~~D. M. S. WATSON, F.R.S.~~ A. J. CLARK

10.30 a.m. *to* **1.0 p.m.**

L. R. Bishop . . .	The Grain Proteins of Barley and related Cereals.
Barbara Russell-Wells .	Fats of the Marsh Forms of *Pelvetia canaliculata.*
J. Needham, D. M. Needham, E. Baldwin *and* J. Yudkin	(*a*) Comparative ~~observations~~ studies on the Phosphagens, with some remarks on the origin of the Vertebrates (*b*) Phosphagen during the embryonic development of *Sepia.*
P. Eggleton . . .	The metabolism of the isolated heart of the Frog.

SECOND SESSION

Friday, December 18th, in the Department of Zoology.

In the Chair: Professor ~~T. G. HILL~~ D. M. S. WATSON

2.15 p.m. *to* **4.0 p.m.**

E. M. Delf . . .	Experiments with stipes of *Fucus* and *Laminaria.*
H. W. Buston . .	The Accessory Factor necessary for the Growth of *Nematospora gossypii.*
D. G. Catcheside . .	The Chromosomes of a new haploid *Oenothera.*

4.0 p.m. *to* **5.30 p.m.** Tea and Demonstrations.

Demonstrations will include:

Dr P. A. Buxton . .	Hygrometric apparatus and charts.
Mr D. G. Catcheside .	The Chromosomes of a new haploid *Oenothera.*
Miss Ruby Dowling .	Broomrape (*Orobanche minor*) on unusual host plants.
Dr R. P. Hobson . .	The effect of yeast extracts on the growth of aseptic blow-fly larvae.
Prof. J. S. Huxley *and* Dr A. Wolsky . .	The Structure of normal and mutant eyes in *Gammarus chevreuxi.*

Reprint of Ergot, inord. papers to AJ Clark

Pharmacol. Lab. Edinburgh

Melanoplus grasshopper

Mr K. Mellanby . .	The regulation of its internal temperature by an insect.
Mr R. Palmer . .	The experimental imitation of a mutant phenotype in *Gammarus chevreuxi.*
Miss R. M. Renton . .	Aquarium Methods.
Prof. H. E. Roaf . .	The action of drugs on invertebrates.
Mr G. P. Wells . .	Colour-response in a leech.
Mr M. J. D. White .	The Sex-Chromosomes of the Fowl.

5.30 p.m. *to* **6.30 p.m.**

Dr P. A. Buxton . .	The water balance of insects.
Dr G. R. Cameron .	Inflammation in *Lumbricidae.*

Mealworm burning stuff to keep itself going in dry air (Mellanby)

Some insects are hygroscopic

THIRD SESSION

Saturday, December 19th, in the Department of Physiology.

In the Chair: Professor H. E. ROAF

10.30 a.m. *to* **1.0 p.m.**

H. E. Roaf . . .	The action of drugs on invertebrates.
H. Munro Fox . .	The reversible stoppage of invertebrate hearts.
Lancelot Hogben *and* Enid Charles . .	The effect of Sexual Excitement and of Anterior Lobe Injections on the Blood-Calcium of Rabbits.
C. M. Yonge . .	The Permeability of Chitin.
J. E. Harris . .	Brownian Movement and the Viscosity of Protoplasm.

FOURTH SESSION

Saturday, December 19th, in the Department of Physiology.

In the Chair: Professor A. E. BOYCOTT, F.R.S.

2.15 p.m. *to* **4.0 p.m.** XXXX

J. Gray	The Locomotion of Fish.

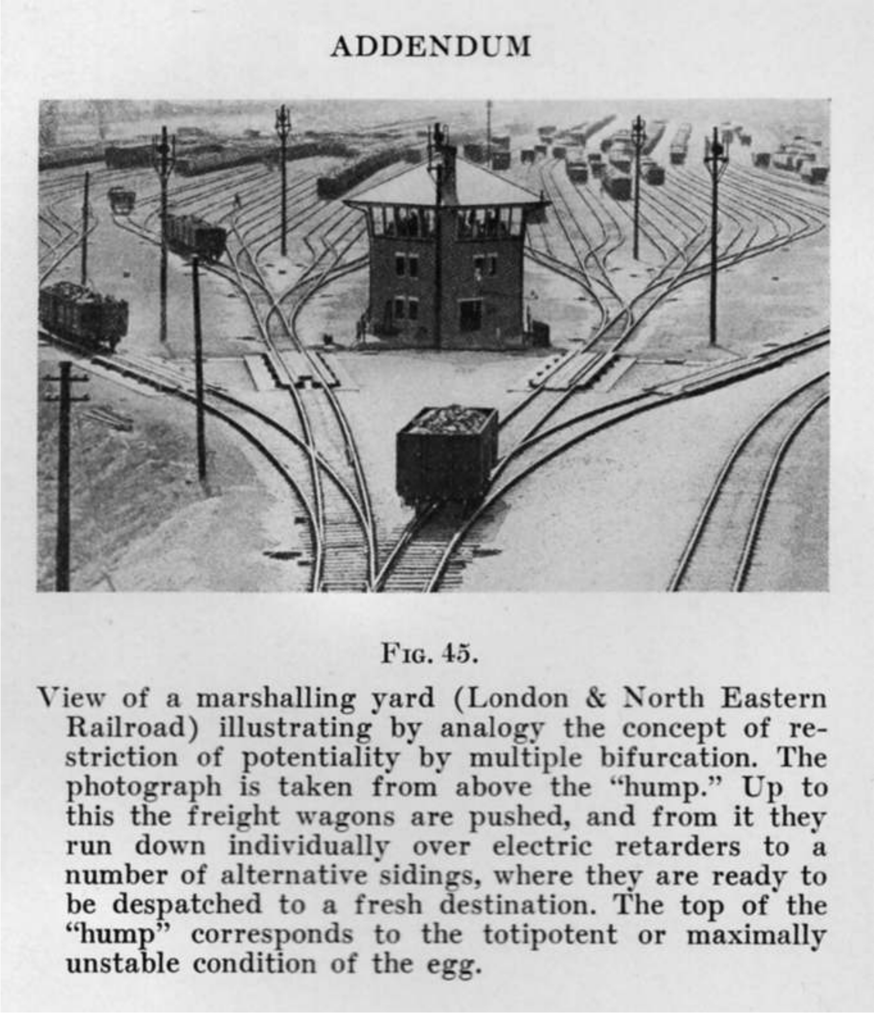
After Mr Gray's paper the Harvey Film will be shown. This film, kindly lent by Professor Lovatt Evans, is based upon Harvey's *De Motu Cordis.*

J. T. Cunningham

FIGURE 1.5: Joseph Needham, *Programme of the Society for Experimental Biology Meeting* in December 1931. Copyright: Cambridge University Library, Department of Manuscripts and University Archives, Joseph Needham Papers, GBR/0012/MS Needham, J.232.

branching out of rail lines from a central distribution point. Needham's enthusiasm for trains is known from anecdotes, relating his childhood love for his model train or the fact that he learned the basics of steering an engine as a schoolboy. During the General Strike in May 1926, he even volunteered as a driver for the British Railways, finding himself on the wrong side of history, as he later reflected.[43]

The deeper meaning behind his doodles becomes evident when one looks into his 1936 book *Order and Life*, which ends with an avant-garde style photograph of the London & North Eastern Railroad Whitemoor Marshalling Yard, printed as an addendum (Figure 1.6). The caption informs the reader that the photograph, first published in 1929, was taken from above the 'hump' of the marshalling yard, from which the wagons roll down to be automatically sorted by shunting switches into a



ADDENDUM

Fig. 45.

View of a marshalling yard (London & North Eastern Railroad) illustrating by analogy the concept of restriction of potentiality by multiple bifurcation. The photograph is taken from above the "hump." Up to this the freight wagons are pushed, and from it they run down individually over electric retarders to a number of alternative sidings, where they are ready to be despatched to a fresh destination. The top of the "hump" corresponds to the totipotent or maximally unstable condition of the egg.

FIGURE 1.6: London & North Eastern Railroad Whitemoor Marshalling Yard, 1929, in: Joseph Needham, *Order and Life*, London, Cambridge: MIT Press, 1936.

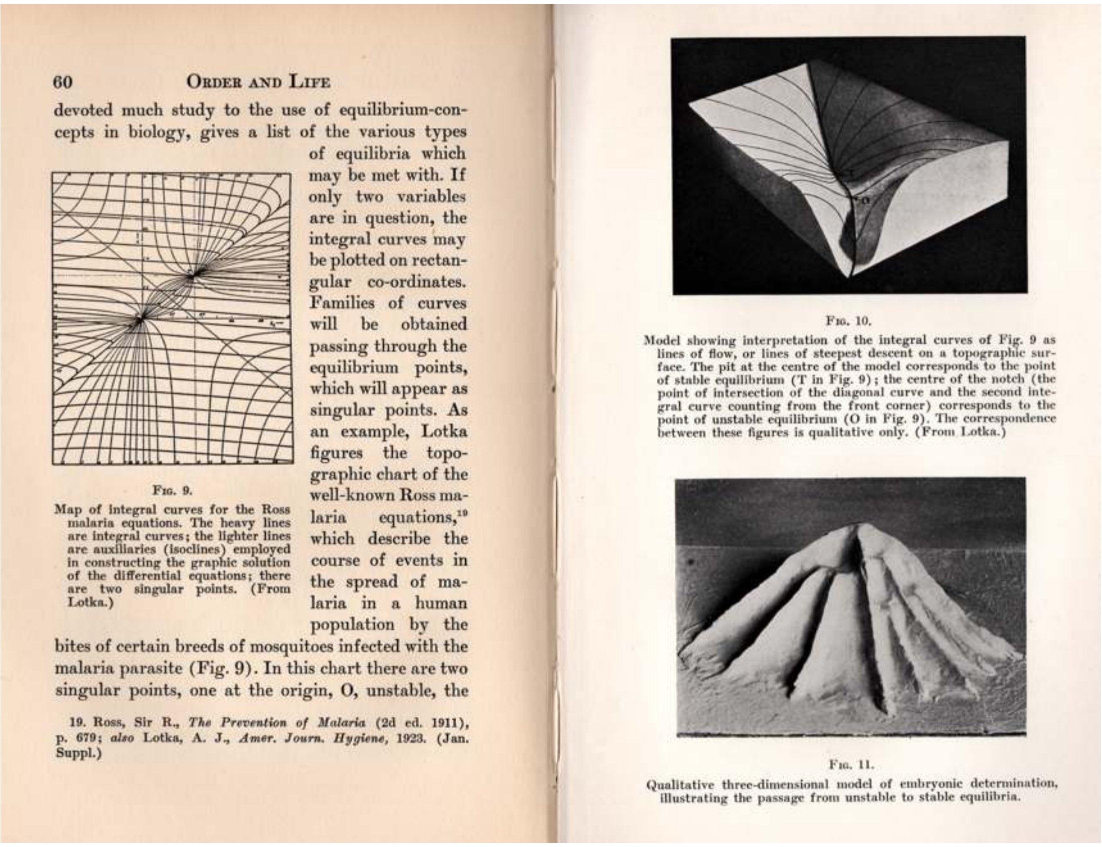
number of alternative sidings, from where they are dispatched to their final destinations. As Needham explains, this pathway corresponds to the restriction of potentiality with each step of bifurcation that the fertilised egg undergoes. The 'hump' itself stands for the unstable state of the totipotent germ cell before it differentiates through cell division, during which the cells' potentiality is incrementally reduced (Needham 1936: addendum, 61f.). Waddington used the identical image as a metaphor in *How Animals Develop*, published in the same year. He spells out the analogy in more detail, comparing the successive points to primary and secondary organisers within the embryo:

> Now an embryo is in some ways analogous to a set of trucks sliding down the Hump. The first point, which you see just in front of the nearest two trucks in the picture, is the primary organisation centre and shunts off one set of trucks to the left, to become skin, and another set to the right to become neural plate. The next set of points are the secondary organisers [...] and they again sort out the neural plate trucks into brain trucks and spinal column trucks, and the skin trucks into lens and epidermis trucks.
> (Waddington 1936: 96f.)

Accordingly, each truck represents a bit of competent tissue, acted on by the organiser to develop in one or the other direction. In case of interference, the points can send the trucks on a different developmental track from the usual one, causing cells that would normally produce skin tissue, for instance, to form lenses.[44] The sorted trucks, aligned in the sidings, represent the final organism with its various types of tissue and organs.

What is missing in this analogy, Waddington however warns, is the representation of a system of levers that coordinates the points throughout the marshalling yard. For in the embryo, the differentiation of a group of cells is not evoked individually, but is coordinated with all other developing tissues. It is by this intricate coordination within what Waddington calls the 'individuation field' that an organism with complex organs emerges. Waddington finds another shortcoming of the analogy in the fact that the trucks are sorted by a man sitting in the control-box using his brains. He identifies this as a major weak-point vulnerable to vitalist interpretation – to the introduction of a 'non-material agency which works just like the man in the control tower' to ensure 'the harmonious development of the different parts of the embryo' (Waddington 1936: 98f.).

At this time, Needham and Waddington were already working on a different metaphor. Accompanying his text in *Order and Life*, Needham published a photograph showing the hand-made clay model of a hillside with grooves (Figure 1.7). He describes how a rolling ball would descend from the position of greatest instability at the summit down a groove in the hillside to the next level of instability, which would again decide about its future direction towards a stable equilibrium. Though a certain cell may usually produce tissue of a certain kind (prospective



60 ORDER AND LIFE

devoted much study to the use of equilibrium-concepts in biology, gives a list of the various types of equilibria which may be met with. If only two variables are in question, the integral curves may be plotted on rectangular co-ordinates. Families of curves will be obtained passing through the equilibrium points, which will appear as singular points. As an example, Lotka figures the topographic chart of the well-known Ross malaria equations,[19] which describe the course of events in the spread of malaria in a human population by the bites of certain breeds of mosquitoes infected with the malaria parasite (Fig. 9). In this chart there are two singular points, one at the origin, O, unstable, the

FIG. 9.

Map of integral curves for the Ross malaria equations. The heavy lines are integral curves; the lighter lines are auxiliaries (isoclines) employed in constructing the graphic solution of the differential equations; there are two singular points. (From Lotka.)

19. Ross, Sir R., *The Prevention of Malaria* (2d ed. 1911), p. 679; *also* Lotka, A. J., *Amer. Journ. Hygiene*, 1923. (Jan. Suppl.)

FIG. 10.

Model showing interpretation of the integral curves of Fig. 9 as lines of flow, or lines of steepest descent on a topographic surface. The pit at the centre of the model corresponds to the point of stable equilibrium (T in Fig. 9); the centre of the notch (the point of intersection of the diagonal curve and the second integral curve counting from the front corner) corresponds to the point of unstable equilibrium (O in Fig. 9). The correspondence between these figures is qualitative only. (From Lotka.)

FIG. 11.

Qualitative three-dimensional model of embryonic determination, illustrating the passage from unstable to stable equilibria.

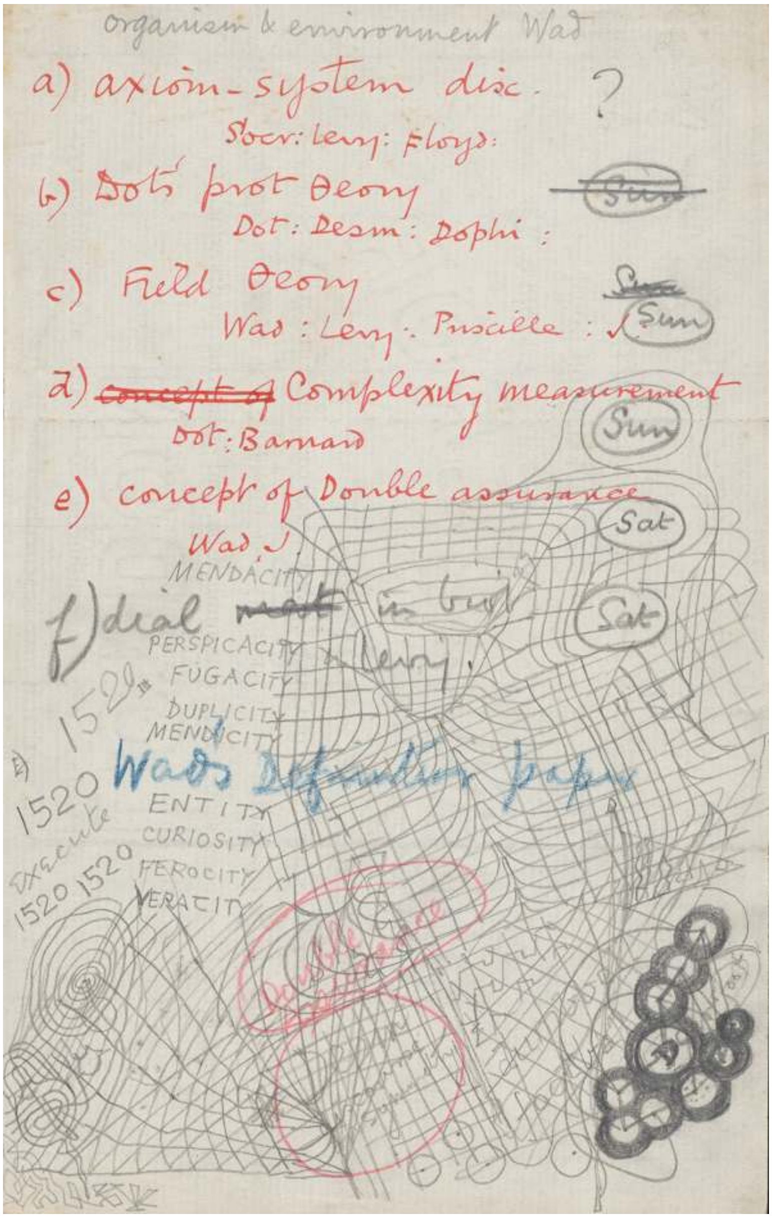
FIGURE 1.7: Alfred Lotka's diagram and model and Joseph Needham's three-dimensional model of embryonic determination, in: Joseph Needham, *Order and Life*, London, Cambridge: MIT Press 1936, p. 60f.

significance), its potentiality is not limited to this one outcome (prospective potency) and it can change routes if needed. The grooves and saddles on the hillside function much like the tracks and the distribution points in the marshalling yard. The decisive advantage of this model, however, lies in the fact that a ball would roll down the slopes of the hill on its own, without a controlling intelligence. Needham refers to Alfred Lotka's topological representation of the Ross malaria equations, dealing with possible developments in the spread of malaria among a human population, as his inspiration. Lotka first plotted these equations on a chart, which revealed two singular points, one of unstable and the other of stable equilibrium. He then interpreted this chart topographically, showing the stable equilibrium point as a valley and the unstable equilibrium as a notch. Critical information could thereby be read from the model intuitively (Needham 1936: 59–61).

What could furthermore have attracted Needham and Waddington to Lotka's model was its literal visualisation of a field. Already Lotka's chart looks much like the visualisation of an electromagnetic force field as developed by James Clerk Maxwell. The field was a central concept with which Waddington and Needham hoped eventually to be able to explain the coordinated differentiation of tissue into organs. The Viennese biologist and trained engineer Paul Weiss had introduced the field concept into biology in 1926 and linked it to Wolfgang Köhler's concept of 'physical gestalten'.[45] For in an electromagnetic field, as in a gestalt, each point is distinguished from every other by location, orientation and intensity. At the same time, there is a relationship between all points, such that a change in the quality of one point alters all the others. This idea became central to Needham's and Waddington's concept of the individuation field, which they had identified as 'a region [of tissue] throughout which some agency is at work in a coordinated way', and thus as a core factor of the embryo's 'Gestaltungsprinzip' or 'Gestaltungsgesetze', its rules of morphogenetic order or design (Needham 1936: 102).[46]

A slip of paper among Needham's notes from the June 1936 meeting of the Theoretical Biology Club, on which he had jotted down the meeting's program – with Waddington's discussion of 'Field Theory' on Sunday – is covered in the lower half by a network of pencil lines (Figure 1.8). While the net is reminiscent of Lotka's chart, the marshalling yard reappears in the branching lines in the lower left-hand corner of the page. However, the tracks have now turned into furrows or channels, making it look as if Needham had tentatively combined the concept of the field with an uneven landscape. In the lower right-hand corner, he has drawn an accumulation of circles outlined first in pencil, then in black marker. The adjacent word 'football' seems to make it admissible to read the circles as spheres. Linking them to the hillside model, they could represent different pluripotent tissues in the developing embryo, headed from a point of unstable equilibrium to a number of distinct differentiated states. As before, a prospective potency is inscribed into the system, allowing the tissue cells to respond to interferences by taking alternative developmental pathways.

The sketch might document the gestalt switch – involved according to Thomas S. Kuhn in paradigm-change (1962: 114)[47] – that paved the way to a more adequate model of the ontogenetic process, replacing the mechanist image of the demiurgically controlled marshalling yard by a field or landscape. In the sketch, the combination of track and topography, field and gestalt is still recognizable, which is partially lost in the clay model (Figure 1.7). And yet, the topographic model, calling to mind familiar Alp reliefs, can be read much more intuitively and is hence remembered more easily – an important asset in an interdisciplinary setting. Already in 1929, Needham had remarked that '[t]he process of a scientific discovery bears strong resemblance to a work of art and is in no minor sense a work of creation' (Needham 1929: 55).[48] Though analogies could at times prove to be dangerous, as they may be misleading, it was more important to choose them well – in a way that



organism & environment Wad

a) axiom-system disc. ?

Sbcr: Levy: Floyd:

b) Dot's prot θeory ~~Sun~~

Dot: Desm: Dophi :

c) Field θeory ~~Sun~~

Wad : Levy : Priscille : ✓ Sun

d) ~~concept of~~ Complexity measurement Sun

Dot: Barnard

e) concept of Double assurance Sat

Wad. J

MENDACITY

f) dial ~~not~~ in big Levy. Sat

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Double assurance

FIGURE 1.8: Joseph Needham, notes concerning the Biotheoretical Gathering in June 1936. Copyright: Cambridge University Library, Department of Manuscripts and University Archives, Joseph Needham Papers, GBR/0012/MS Needham, J.246.

the associations they call to mind correspond to the relevant elements of the subject of research. If this is the case, an analogy could even advance research by offering a coordinate system for a meaningful organisation of disparate observations. As Jan Baedke has shown, a visual metaphor is either fuzzy at the beginning and can be further elaborated through research guided by the analogy, or it is over-defined in the sense that it contains more details than the knowledge we have of the object of scientific interest. Testing whether these additional aspects are relevant to the analogy can produce new research questions and unexpected insights.[49]

It seems to have been this quality of the topographical model that Waddington recognised as potentially productive for his own work in epigenetics. His first adaptation of the landscape metaphor appeared in 1940 in *Organisers and Genes* (Figure 1.9). Surprisingly, it does not show a diagrammatic representation, but a landscape drawing by the artist John Piper. Printed as a frontispiece to his book, the drawing, presumably made with charcoal originally, shows a river delta. A rushing stream runs through valleys towards the sea, with side-streams branching off at intervals, while the riverbanks become increasingly steep and canyon-like. Wavy, serpentine lines signal a strong river current, while energetic scribbles on the adjacent fields seem to mark weathered brushes of the heath and the wind blowing through the grasslands. In the background wind-born clouds pass by, heavy with rain.

Below the image, Waddington has added the caption ‘The Epigenetic Landscape’, identifying the drawing as the central visual metaphor for his theory of epigenetics. In contrast to most western geneticists of his time, who were convinced that the organismal phenotype is determined by genes, Waddington believed in the relevance of the cell plasma and external conditions. This called for a variety of developmental pathways that could be taken in reaction to influences from both within and without. At the same time, the further an embryo is differentiated, the less it is able to respond to disturbances – hence, the canyons surrounding the river in ‘The Epigenetic Landscape’ become steeper towards the water mouth, channelling the stream more rigidly.

While the image maintains all the relevant aspects of the marshalling yard, the landscape as a literal ‘field’ represents a counter-image to the machine. Instead of wagons controlled by a human being, or a sphere rolling down a hill unnaturally, the water runs down the gorges on its own. It is the topography itself, analogous to the individuation field, that directs the water into different channels. A major advantage over the mountain model is the processuality of the image: the rough charcoal scribbles, whirls and waves create a sense of movement in the eye of the beholder. In *Organisers and Genes*, Waddington writes about the image, which was the product of a collaboration with Piper: ‘It is an amusing landscape to picture to oneself, and I think it expresses, formally at least, some characteristics of development which are not easy to grasp in any other way’ (1940: 93).[50] As the multidimensional space of metabolism was ‘not very easy for the simple-minded biologist to imagine or think about’, Waddington deemed it necessary to resort to a two-dimensional model ‘to form rather an intuitive picture of it, rather than a precise delineation’ (1957: 51).[51] Apparently, the organicist synthesis in

THE EPIGENETIC LANDSCAPE

From a drawing by JOHN PIPER

Looking down the main valley towards the sea. As the river flows away into the mountains it passes a hanging valley, and then two branch valleys, on its left bank. In the distance the sides of the valleys are steeper and more canyon-like. (See p. 91.)

FIGURE 1.9: John Piper, *The Epigenetic Landscape*, in: Conrad H. Waddington, *Organisers and Genes*, Cambridge: Cambridge University Press, 1940, frontispiece.

embryology to him was captured in this concrete drawing, including the specificity of its medium and materiality. Only in 1957 in *The Strategy of the Genes* did Waddington publish a diagrammatic rendering of the epigenetic landscape (Figure 1.10), now linking the mountain-relief style topography representing the action of organisers and evocators in individuation fields to an underlying genetic control,

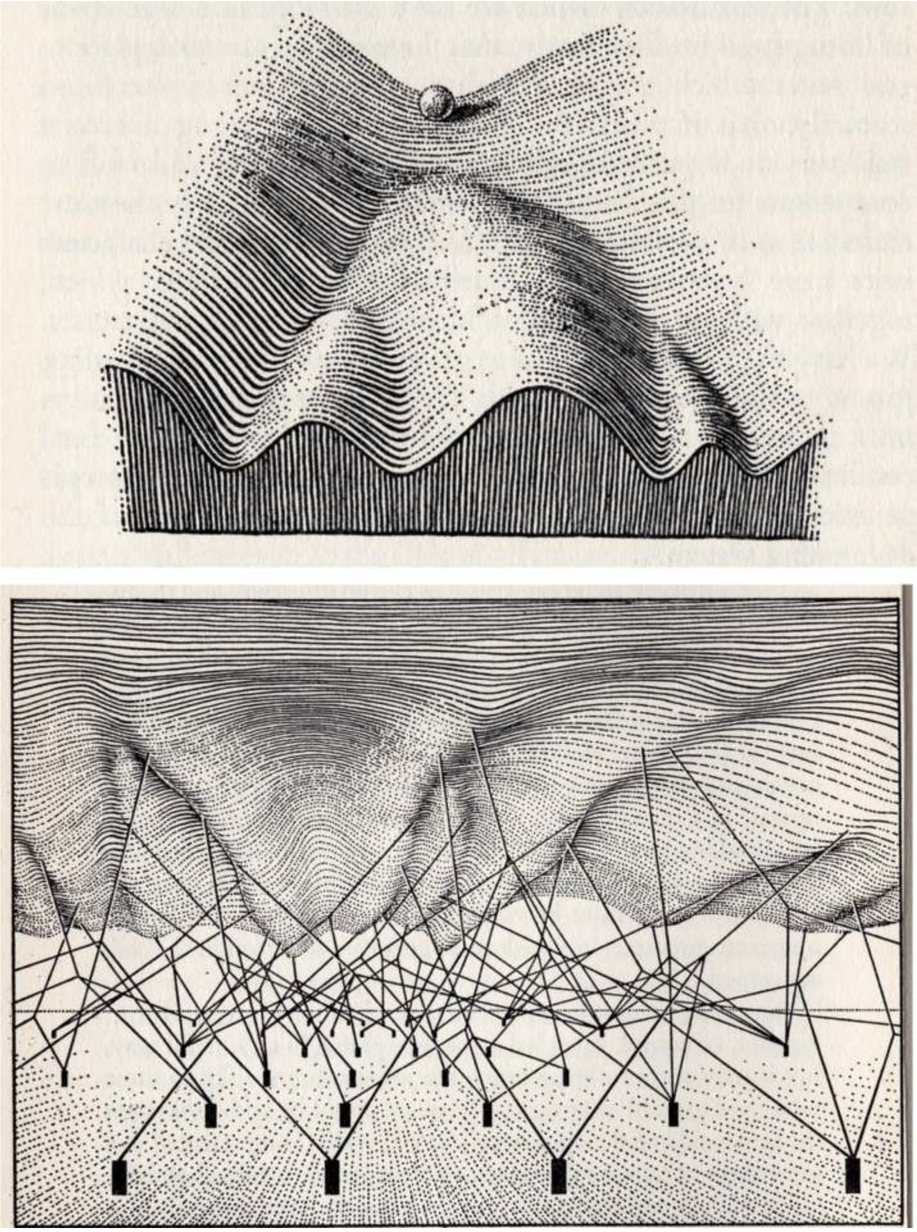

FIGURE 1.10: Diagrams of the epigenetic landscape, in: Conrad H. Waddington, *The Strategy of the Genes*, London: Allen & Unwin, 1957, pp. 29, 36.

interacting bottom-up as well as top-down. The curvature of the surface, the sphere rolling down the slope and the wires below appear to have been taken directly from the sculptures and drawings by Hepworth, Moore and Gabo that Waddington would have seen regularly during the mid to late 1930s as well as after the war.

But why did Waddington, the early and fervent supporter of abstraction in art, first choose a surrealist landscape depiction? Created shortly after the British entry into the World War Two and in the year of The Blitz, Piper's drawing shows a dystopian, post-apocalyptic landscape. Only in 1938 had Piper returned to realism against the background of increasing political tensions and impending war. As Waddington relates in his book *The Scientific Attitude* of 1941, abstraction now seemed too inaccessible, too 'flimsy' and apolitical to make a socially relevant contribution through art: 'One wants something more, one wants to get hold of real things again' (1948: 47f.).[52] Piper returned to the landscapes and seascapes of his homeland that he had been occupied with in the early 1930s, creating collages with objects he found on the beach. It may have been this technique of integrating the environment into the representation of organic nature that predestined him for a visualisation of the epigenetic landscape in Waddington's eyes. Between 1937 and 1939, Piper worked on two Shell travel guides through England, for which he studied British topographies, painting mountains for the first time in 1939. These landscapes, however, were decidedly darker than his earlier works. In early 1940, he was made an official war artist and commissioned to paint inside Air Raid Precaution control rooms, before receiving a mandate to document bombed churches and other buildings, which he would visit on the morning after an air raid. As a war artist, Piper's work partook in a patriotic, anti-war agenda. This adds a layer of social engagement to Waddington's landscape that was wholly in accordance with the biologist's intentions. Not only was Waddington himself involved in the war effort, contributing to operational research with the Royal Air Force and, in 1944–45, acting as scientific advisor to the Commander in Chief of Coastal Command.[53] He also welcomed Piper's return to representational painting as he believed it brought artists back in touch with the 'interests of their fellow men', an idea reflecting his socialist politics (Waddington 1941–48: 48).

Yet, Piper, like Waddington, also saw a strong connection between his abstract and more representational works, claiming that a sense of form, rhythm and tectonics trained in abstraction also informed his topographical paintings and collages (Jenkins and Spalding [2003: 54]; Jenkins [2001: 16]; Waddington [1969: 55]). Despite Waddington's war-time doubts regarding abstraction, Piper's Constructivist works had had a special relevance to him. The biologist and his wife, Justin Blanco White, owned several of Piper's abstract paintings, among them the one depicted on a colour plate in *Behind Appearance* (Figure 1.11). As Waddington points out in his book, its rectangular forms in brilliant colours interpenetrate each other with protruding half-circles and pointed extensions, in a continuous redistribution of space and preponderance, vying for the beholder's attention. Waddington interpreted these colour planes as interacting fields of force and found aspects of his own scientific preoccupations reflected therein: 'This sense of the real world as an area of interlocking energies, of a line as a path of minimum energy through orderly fields of force, is, of course, an expression of some of the basic notions of modern science' (Waddington 1969: 55). Apparently Piper's abstract

FIGURE 1.11: Abstract painting by John Piper, in: Conrad H. Waddington, *Behind Appearance. A Study of the Relations Between Painting and the Natural Sciences in this Century*, Edinburgh: Edinburgh University Press, 1969, p. 56. © The Piper Estate.

paintings had helped him get a better grip on certain concepts he was working on at the time in the context of embryology.

However, in the context of the publication of *Organiser and Genes*, with which Waddington hoped to convince a broad readership of the relevance of interacting forces on the developing organism as a whole, a more earthy and intuitive image seems to have appeared more to the point than an abstraction. As he writes in *The Scientific Attitude*, an 'abstract picture is too indirect a way of approaching people', later commenting that geometric art has 'rather limited appeal' to most beholders (Waddington 1941-48: 47).[54] Especially in an interdisciplinary context, a realistic metaphor may have made it easier for scientists coming from different fields (geneticists, embryologists, biochemists, etc.) to relate to the model and find a shared vocabulary (e.g. 'canalisation') to discuss the developmental process (Baedke 2016: esp. 183–85). Even if Waddington would later find the ideal visualisation of the new organicist world picture in Abstract Expressionism, in the war year 1940, he seems to have preferred an image that represents science as less cold and exclusive and more accessible and relevant to the world of experience. Abstraction suddenly appeared as a 'caricature of the scientist as the depersonalised researcher in a white coat' (Waddington 1969: 58).[55] The apocalyptic connotations of the drawing may also have been a monition to scientists not to forget their ethical responsibility.

Despite these reservations about abstraction, it was the diagrammatic model of the epigenetic landscape (Figure 1.10) that had the most successful afterlife, still being used today to visualise theories of unidirectional development from unstable or high-energy levels to more stable states.[56] What is no longer apparent is the 'epigenetic' relationship of these images to British Constructivism of the 1930s – to the wire sculptures and the spherical, crystalline and organic forms of Barbara Hepworth, Henry Moore, Naum Gabo, Ben Nicholson and John Piper. It was their 'effort of the imagination', however, that helped to instil new models and concepts in budding organicist or process biology. This thread has been taken up again today in the collaborative drawing lab research initiated by artist Gemma Anderson-Tempini, biologist James Wakefield and philosopher of science John Dupré, helping scientists gain a similarly strengthened intuitive grasp of complex biological processes.

NOTES

1. Waddington, Conrad H. (1969), *Behind Appearance. A Study of the Relations between Painting and Natural Sciences in this Century*, Edinburgh: Edinburg University Press.
2. Arnheim, Rudolf (1970), 'He knows the arts from the inside', in *The Book Guide*, p. 6. Conrad H. Waddington Papers, Edinburgh University Library Special Collections, GB 237 Coll-41/2/2/5.
3. See for instance: Bronowski, Jacob (1958), 'The creative process', *Scientific American* 199:3, September, pp. 58–65; and Bronowski, Jacob (1960), 'Art and science II. A portfolio of forty paintings, drawings, and photographs', in *The Scientific American*; Georg Schmidt, *Form in Art and Nature*, ex. cat., Kunsthalle Basel, Basel 1958. In 1968, the scientist and artist Frank Malina, who corresponded with Waddington, founded the journal *Leonardo* dedicated to aspects of science and technology in art. Regarding the idea that art can enhance the scientific quest, Waddington was altogether closer to György Kepes, with whom he collaborated in the context of the 'Vision and Value' series. On the relevance of meetings with British organicist biologists for Kepes, see Roach, Leigh Anne (2010), 'A positive, popular art: Sources, structure, and impact of György Kepes's language of vision', Ph.D. dissertation, Florida State University.

4. Kuhn, Thomas S. (1962), *The Structure of Scientific Revolutions*, Chicago: University of Chicago Press.
5. Waddington, Conrad H. (1951), ‘The character of biological form’, in L. Law Whyte (ed.), *Aspects of Form. A Symposium on Form in Nature and Art*, London: Percy Lund Humphries (2nd ed. 1961), pp. 43–56, here p. 44.
6. Boehm, Gottfried (2018), ‘Kraftfeld. Versuch über eine ikonische Kategorie’, in F. Fehrenbach, R. Felfe and K. Leonhard (eds), *Kraft, Intensität, Energie. Zur Dynamik der Kunst*, Berlin: De Gruyter, pp. 355–71, here p. 366f.
7. Cf. Henderson, Linda Darymple (1983), *The Fourth Dimension and Non-Euclidean Geometry in Modern Art*, Princeton: Princeton University Press.
8. Arnheim, Rudolf (1951–1961), ‘Gestalt psychology and artistic form’, in Whyte, pp. 196–208, here p. 196.
9. Arnheim, Rudolf (1951–1961: 203). Köhler, Wolfgang (1920), *Die physischen Gestalten in Ruhe und im stationären Zustand*, Brunswick: Fr. Vieweg & Sohn.
10. Arnheim, Rudolf (1943), ‘Gestalt and art’, *The Journal of Aesthetics and Art Criticism* 2:8, Autumn, pp. 71–75, here p. 73.
11. See letter from Waddington to Arnheim, 30 August 1970, Waddington Papers, University of Edinburgh, GB 237 Coll-41/2/2/5.
12. As papers in his archive convey, Joseph Needham, with whom Waddington was collaborating at the time, was interested in biological field theory in the early 1930s, taking note of German publications on the topic such as Weiss, Paul (1926), *Morphodynamik. Ein Einblick in die Gesetze der organischen Gestaltung anhand von experimentellen Ergebnissen*, Berlin: Gebrüder Borntraeger; or Rudy, H. (1930), *Die biologische Feldtheorie*, Berlin: Gebrüder Borntraeger. Joseph Needham Papers, Cambridge University Library Special Collections, GBR/0012/MS Needham, J.246. See also Needham’s discussion of biological fields and ‘physische Gestalten’ in *Order and Form*, p. 70 and pp. 81–102. Joseph Woodger, initiator of the Theoretical Biology Club meetings, translated Ludwig von Bertalanffy’s *Theoretische Biologie* (1932) into English and was influenced by his *Kritische Theorie der Formbildung* (1928), both dealing with these concepts.
13. Peterson, Erik L. (2016), *The Life Organic. The Theoretical Biology Club and the Roots of Epigenetics*, Pittsburgh: University of Pittsburgh Press, p. 130.
14. Wittgenstein, Ludwig (2001), *Philosophische Untersuchungen. Kritisch-genetische Edition*, ed. by Joachim Schulte, Frankfurt a.M, p. 1044 (my translation). This idea was also upheld by modernist artists such as Paul Klee and Wassily Kandinsky, see for instance: Fehrenbach, Frank, Felfe, Robert and Leonhard, Karin (2018), ‘Die Kräfte der Künste. Zur Einleitung’, Fehrenbach/Felfe/Leonhard, pp. IX–XIX.
15. Vischer, Robert (1873), *Über das optische Formgefühl. Ein Beitrag zur Aesthetik*, Leipzig: Credner; Lipps, Theodor (1906), ‘Einfühlung und ästhetischer Genuss’, *Die Zukunft* 54, pp. 108; Wölfflin, Heinrich (1886), *Prolegomena zu einer Psychologie der Architektur*, Berlin: Schwabe; Lee, Vernon, and Anstruther-Thomson, Clementina (1897), ‘Beauty and Ugliness’,

Contemporary Review 72, October, pp. 544–69. For a history of the concept of ‘empathy’, see: Maskarinec, Malika (2021), ‘Formkräfte in der Einfühlungsästhetik um 1900’, in Frank Fehrenbach et al. (ed.), *Form- und Bewegungskräfte in Kunst, Literatur und Wissenschaft*, Imaginarien der Kraft, vol. 2, Berlin: De Gruyter, pp. 97–115; Koss, Juliet (2006), ‘On the Limits of Empathy’, in *The Art Bulletin* 88:1, March, pp. 139–57; Ziebritzki, Jo (2021), ‘Wie die eigene Wahrnehmung zu wissenschaftlicher Erkenntnis wird: untersucht anhand von Lees und Anstruther-Thomson “Beauty and Ugliness” (1897)’, *Kritische Berichte* 49:4, pp. 50–62.

16. Read, Herbert (1931), *The Meaning of Art*, London: Faber & Faber (2nd ed. 1936).
17. Recent research on image perception has found astonishing evidence of such subliminal activation: Lauschke, Marion, Nyakatura, John, Casper, Mac-Oliver et al. (2018), ‘The movement-image compatibility effect: Embodiment theory interpretations of motor resonance with digitised photographs, drawings, and paintings’, *Frontiers in Psychology*, 9, June.
18. Rosenberg, Harold (1952), ‘The American action painters’, *ARTnews*, December, pp. 22f. and pp. 48–50.
19. This was also the first painting for which Pollock abandoned the easel to work on the floor, see Hickey, Jennifer, ‘MoMA’s Jackson Pollock Conservation Project’, *Inside/Out*, MoMA/MoMA PS1 Blog, https://www.moma.org/explore/inside_out/2013/07/18/momas-jackson-pollock-conservation-project-number-1a-1948/. Accessed 10 September 2021.
20. Vogel, Carol (2013), ‘A Pollock restored, a mystery revealed’, *New York Times*, 27 May 2013, https://www.nytimes.com/2013/05/28/arts/design/jackson-pollocks-one-number-31-1950-restored-by-moma.html. Accessed 10 September 2021. It is known that Pollock read and valued D’Arcy W. Thompson’s book *On Growth and Form*, which outlines a neo-mechanist theory, according to which regular forms in inorganic and organic nature as well as in art are produced by physical forces.
21. On the reverberations of these ideas in Vienna, where Hans Przibram, Paul Weiss, and Ludwig von Bertalanffy belonged to the founders of organicist biology, see Coen, Deborah R. (2007), *Vienna in the Age of Uncertainty. Science, Liberalism, and Private Life*, Chicago, London: University of Chicago Press; Coen, Deborah R. (2006), ‘Living precisely in Fin-de-Siècle Vienna’, *Journal of the History of Biology*, 39, pp. 493–523. D’Arcy Thompson also believed that a fundamental indeterminacy was central to uniting biology and physics.
22. Papers of Conrad H. Waddington, Edinburgh University Library Special Collections, GB 237 Coll-41/2/1/2.
23. Hadamard, Jacques (1945), *An Essay on the Psychology of Invention in the Mathematical Field*, Mineola: Dover Publications Inc.
24. In Gemma Anderson-Tempini’s Drawing Labs, it was also observed that the scientists developed a more intuitive understanding of the processes they were working on.
25. Incidentally, also in Gemma Anderson-Tempini’s Drawing Lab, on Intrinsically Disordered Proteins, gestural drawings reminiscent of Jackson Pollock’s drip paintings and Willem de

Kooning's ink drawings were developed to approximate the complexity of spatial structure. In *On Growth and Form*, D'Arcy Thompson had in a similar vein reflected on the near-organic complexity produced in marbled paper by the action of simple physical forces and chance effects. See Thompson (1917: 736f).

26. Cassirer, Ernst (1982), *Philosophie der symbolischen Formen* (Philosophy of Symbolic Forms), vol. III, Darmstadt: Wiss. Buchgesellschaft, p. 235; Waddington (1969: ix); Waddington, Conrad H. (1968), 'New Visions of the World', in *Leonardo* 1:1, January, pp. 69–75, here p. 72.
27. Letter from Ernst Gombrich to C. H. Waddington, 30 December 1969, Papers of Conrad H. Waddington, Edinburgh University Library Special Collections, GB 237 Coll-41/2/2/5.
28. His contacts become clear from correspondence an notes in his archive at Edinburgh University Library Special Collections. For Herbert Read's theory of art, see Thistlewood, David (1984), *Herbert Read. Formlessness and Form. An Introduction to his Aesthetics*, London: Routledge & Kegan Paul; Juler, Edward (2015), *Grown But Not Made. British Modernist Sculpture and the New Biology*, Manchester: Manchester University Press. On biocentrism, see Botar, Oliver A. I. and Wünsche, Isabel (2011), *Biocentrism and Modernism*, New York: Ashgate Publishing; and Mundy, Jennifer (1984), 'Form and creation: The impact of the biological sciences on modern art', in *Creation. Modern Art and Nature*, ex. cat., Edinburgh: Scottish National Gallery of Modern Art, pp. 16–23; Geiger, Annette, Hennecke, Stefanie and Kempf, Christin (eds) (2005), *Spielarten des Organischen in Architektur, Design und Kunst*, Berlin: Dietrich Reimer.
29. Haraway, Donna (1976), *Crystals, Fabrics, and Fields. Metaphors of Organicism in Twentieth-Century Developmental Biology*, New Haven: Yale University Press.
30. For Spemann's and the Mangolds's work on the organiser and the Needhams's and Waddington's visit to Berlin, see Gilbert, Scott F. (1991), 'Induction and the origins of developmental genetics', S. F. Gilbert (ed.), *Developmental Biology. A Comprehensive Synthesis*, vol. 7, New York, London: Plenum Press, pp. 181–206.
31. On the founding and discussions of the Theoretical Biology Club, see Haraway (1976: 101–43); Abir-am, Pnina G. (1987), 'The biotheoretical gatherings, trans-disciplinary authority and the incipient legitimation of molecular biology in the 1930s: New perspective on the historical sociology of science', *History of Science*, 25, March, pp. 1–70; Abir-am, Pnina G. (1987), 'The philosophical background of Joseph Needham's work in chemical embryology', in Gilbert (1991: 159–80); Peterson (2016: 104–16). For the origins of theoretical and organicist biology in German and Viennese Entwicklungmechanik, see Müller, Gerd B. (Hg.) (2017), *Vivarium. Experimental, Quantitative, and Theoretical Biology at Vienna's Biologische Versuchsanstalt*, Cambridge: MIT Press; Esposito, Maurizio (2011), 'Between holism and reductionism: Organismic inheritance and the Neo-Kantian biological tradition in Britain and the USA, 1890–1940', Ph.D. thesis, Leeds: University of Leeds.
32. From the papers presented by the Russian delegates, especially Boris Hessen's talk on the relevance of early modern mechanics and mercantilism to the development of Newtonian

science left a deep imprint on left-wing historians of science in Great Britain. Cf. *Science at the Crossroads. Papers from the Second International Congress for the History of Science and Technology held in London from June 29th to July 3rd*, London 1931; 2nd ed. 1971 with an introduction by Joseph Needham.

33. See also Bernal, John Desmond (1946), *Science and the Humanities*, London; Bernal, John Desmond (1952), *Marx and Science*, London: Lawrence & Wishart; Bernal, John Desmond (1953), *Science, Industry, and Society in the Nineteenth Century*, Copenhagen; Bernal, John Desmond (1954), *Science in History*, London: Watts. Needham also took an externalist approach to the philosophy of science early on and in the 1940s began to develop his multi-volume, on-going encyclopaedia *Science and Civilisation in China* (1954–present) on this premise. Cf. Needham, Joseph (1926), 'Mechanistic biology and the religious consciousness', in J. Needham (ed.), *Science, Religion and Reality*, New York; Needham, Joseph (1929), *The Sceptical Biologist (Ten Essays)*, London; Needham, Joseph (1971), 'Introduction', in *Science at the Crossroads*, London; Needham, Joseph (2000), 'Foreword', in Zilsel, Edgar (2000), *The Social Origins of Science* (ed. D. Raven, W. Krohn and R. Cohen), Dordrecht, pp. xi–xiv.
34. The texts first appeared in *World Review*, a journal edited by Marcus Brumwell, co-founder of the Design Research Unit, and aimed to apply 'the utopian spirit of Constructivism to plans for the physical and social reconstruction of Britain'. See Burstow, Robert (2014), 'Geometries of hope and fear: The iconography of atomic science and nuclear anxiety in the modern sculpture of World War and Cold War Britain', in C. Jolivette (ed.), *British Art in the Nuclear Age*, London: Taylor & Francis Ltd, pp. 51–79, here p. 61.
35. Waddington, Conrad H. (1944), 'Life from a new angle', in J. R. M. Brumwell (ed.), *This Changing World. A Series of Contributions by Some of our Leading Thinkers, to Cast Light upon the Pattern of the Modern World*, London: Routledge, pp. 39–48, here p. 39.
36. Hepworth appreciated Bernal's criticism, writing to him in a letter: 'Your criticism is most stimulating because you know exactly where a law has been broken + can apply the principle so that you can make the solution clear'. At the same time, she believed that 'we know those laws emotionally + intuitively, learning by our experience + trying to live the sort of life that will most easily enable us to express the laws – that is construction'. Hepworth also sympathised with Bernal's communist efforts and his agenda to reunite art and science and make them relevant to modern society. She hence invited him to write the foreword for the catalogue of her first solo exhibition held at the Lefevre Gallery in October 1937. Burstow (2014: 55). See also Clayton (2021: 76 and pp. 85–87); Barlow, Anne (1996), 'Barbara Hepworth and science', in D. Thistlewood (ed.), *Barbara Hepworth Reconsidered*, Liverpool: Liverpool University Press, pp. 95–107; Brown, Andrew (2005), *J. D. Bernal. The Sage of Science*, Oxford: Oxford University Press, pp. 153f.; Goldsmith, Maurice (1980), *Sage. A Life of J. D. Bernal*, London: Hutchinson, p. 86f.
37. Bernal, John Desmond (1937), 'Art and the scientist', in B. Nicholson, N. Gabo and L. Martin (eds), *Circle: International Survey of Constructive Art*, London: Faber & Faber Ltd., pp. 119–29, here p. 119 and p. 122.

38. See also Thistlewood (1982), ‘Organic art and the popularisation of a scientific philosophy’, *The British Journal of Aesthetics*, 22:4, Autumn, pp. 311–21.
39. Read, Herbert (1955), *The Philosophy of Modern Art*, New York: World Pub. Co., p. 54; Thistlewood (1984: 100). For Moore’s early discovery of Thompson, see Jarron, Matthew (2015), ‘*Independent and Individualist*’. *Art in Dundee 1867–1924*, Dundee & Perth, p. 165. In a letter to D’Arcy W. Thompson of 14 March 1942, Read asks Thompson whether he ever thanked him for the enlightenment he got from his book *On Growth and Form*, which he had already referenced in *Art and Industry* in 1934, and again in his autobiographical *Annals of Innocence and Experience* in 1940. The new edition of *On Growth and Form* was published on 15 June 1942. D’Arcy W. Thompson Papers, University of St. Andrews Special Collections, ms 19379; Read, Herbert (1934), *Art and Industry. The Principles of Industrial Design*, London: Faber & Faber, p. 57; idem. (1940), *Annals of Innocence and Experience*, London: Faber & Faber, pp. 202f.; see also Juler (2015: 35).
40. Thistlewood, David (1996), ‘Contested significance in the work of Barbara Hepworth: Absolute and relativist interpretations’, in Thistlewood (1996: 2–16, here p. 15). Moore may well have discussed Thompson’s ideas with Hepworth while they were students in Leeds and made the biologist’s work familiar to the Hampstead group of artists before 1942, perhaps while he was working on his ‘Transformation Drawings’ inspired by *On Growth and Form* in the early 1930s. Cf. Barlow (1996: 102).
41. Letter from Hepworth to Read, 8 April 1942; op. cit. Thistlewood (1984: 86). Gabo wrote to Read in 1943: ‘Any thing or action which enhances life, propels it and adds to it something in the direction of growth, expansion and development, is Constructive’. Letter from Gabo to Read of 1943, published in *Horizon*, X, 55, July 1944, pp. 57–65.
42. Cambridge University, Archive, Joseph Needham Papers, J.234–5.
43. Wersky (1978: 94); Goldsmith, Maurice (1995), *Joseph Needham. 20th-Century Renaissance Man*, Paris, p. 21.
44. The origin of this work on developmental pathways lies in the famous experiment by Hans Driesch in which he separated cells in the two-cell stage of the embryo and, instead of obtaining two half-embryos, two complete organisms emerged. See Harrington, Anne (1996), *Reenchanted Science: Holism in German Culture from Wilhelm II to Hitler*, Princeton: Princeton University Press; Maienschein, Jane, *The Origins of Entwicklungsmechanik*, in Gilbert (1991: 43–61, here pp. 51f.).
45. Weiss, Paul (1926), *Morphodynamik. Ein Einblick in die Gesetze der organischen Gestaltung an Hand von experimentellen Ergebnissen*, Berlin: Gebrüder Borntraeger; Weiss, Paul (1928), ‘Morphodynamische Feldtheorie und Genetik’, in *Zeitschrift für inductive Abstammungs- und Vererbungslehre*, supplement 2, pp. 1567–74. On Paul Weiss, see Drack, Manfred (2007), ‘On the making of a sytem theory of life: Paul A. Weiss and Ludwig von Bertalanffy’s conceptural connection’, *The Quarterly Review of Biology*, 82:4, December, pp. 349–73. Weiss also published on art and science, for instance: Drack, Manfred

(1955), 'Beauty and the beast: Life and the rule of order', *The Scientific Monthly*, 81:6, pp. 286–99; Drack, Manfred (1960), 'Organic form: Scientific and aesthetic aspects', in G. Kepes (ed.), *Visual Arts Today*, pp. 181–94; Drack, Manfred (1973), *The World of Art*, Carbondale: Southern Illinois University Press; Drack, Manfred (1992), *Creative Ventures*, Carbondale: Southern Illinois University Press.

46. See also Needham, Joseph (1942), *Biochemistry and Morphogenesis*, Cambridge: Macmillan Co. (2nd ed. 1950: 128). The terms 'Gestaltungsprinzip' and 'Gesaltungsgesetz' were adopted from Ludwig von Bertalanffy: von Bertalanffy, Ludwig (1933), *Kritische Theorie der Formbildung*, translated and adapted by Joseph H. Woodger as: *Modern Theories of Development. An Introduction to Theoretical Biology*, London: Oxford University Press. See also von Bertalanffy, Ludwig (1926), 'Zur Theorie der Organischen "Gestalt"', *Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen*, 108:2, pp. 413–16.
47. Like Wittgenstein, Kuhn uses psychologist Joseph Jastrow's Duck-Rabbit as his example, which was also discussed by art historian Ernst Gombrich in *Art and Illusion* in 1959. Gombrich and Kuhn corresponded on the gestalt switch between August and October 1963. Thomas S. Kuhn Papers, MC 240, Box 4, Cambridge: MIT Institute Archives and Special Collections.
48. Needham, Joseph (1929), 'Science and Religion', in Needham (1929: 55).
49. Baedke, Jan (2016), 'Visual metaphors in the sciences: The case of epigenetic landscape images', *Journal for General Philosophy of Science*, 48, August, pp. 173–94, esp. pp. 176f. and pp. 185–89. This effect was also observed in Anderson-Tempini's Drawing Labs.
50. Waddington, Conrad H. (1940), *Organisers and Genes*, Cambridge: Cambridge University Press, p. 93. The participants of Anderson-Tempini's Drawing Labs made very similar observations regarding the images they collaboratively produced.
51. Waddington, Conrad H. (1977), *Tools for Thought*, London: Jonathan Cape Ltd., p. 105. See also Baedke (2016: 183).
52. Waddington, Conrad H. (1948), *The Scientific Attitude* (1941), 2nd revised ed., London: Penguin, pp. 47f. This return to greater realism was also reflected in *AXIS*, a journal for abstract art edited by Myfanwy Piper: after Mussolini's invasion in Abyssinia in 1935, it asked whether abstraction or surrealism should be the style to follow. The last issue appeared in 1937, as belief in abstraction had been relinquished. Piper claimed that '[p]ure abstraction is undernourished. It should at least be allowed to feed on a bare beach with tins and broken bottles'. Jenkins, David Fraser and Spalding, Frances (2003), *John Piper in the 1930s. Abstraction on the Beach*, London, pp. 47f. See also Jenkins, David Fraser (2001), *John Piper: The Forties*, London, New York: Phillip Wilson Publishers, p. 16.
53. Also other members of the Theoretical Biology Club actively contributed to the war on fascism: Bernal, for instance, worked for the Home Office and the Bomber Command and later became Lord Mountbatton's scientific advisor in Combined Operations. Dorothy Needham worked in malnutrition campaigns and stood as Labour candidate for the City Council. Cf. Wersky, Gary (1978), *The Visible College. The Collective Biography of British Scientific Socialists of the 1930s*, New York: Allen & Unwin, p. 219 and pp. 262ff.

54. On purely geometric art, Waddington writes in *Behind Appearance*:

> We have lost all sense of man as an animal, muscular, sexual, and demanding food and drink; or man as a personality or social being; or as an inhabitant of a world of nature filled with burgeoning plant and animal life, or surrounded by architecture fashioned by human hands; standing on soil, rock or tarmac and roofed over by the sky. He is reduced to an incorporeal intelligence imbued with an emotional reaction to the products of his own conceptualising thought. It was mainly in this direction that the geometricising art of the twenties and thirties tended, and many later artists have done so too.
>
> (1969: 58)

55. See also Baedke (2016).
56. Baedke, Jan (2013), 'The epigenetic landscape in the course of time: Conrad Hal Waddington's methodological impact on the life sciences', *Studies in History and Philosophy of Biological and Biomedical Sciences*, 44, pp. 756–73; Baedke, Jan (2018), *Above the Gene, Beyond Biology. Towards a Philosophy of Epigenetics*, Pittsburgh: University of Pittsburgh Press; Squier, Susan Merril (2017), *Epigenetic Landscapes. Drawings as Metaphor*, Durham: Duke University Press.

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2

Drawing as a Pragmatist Visual Epistemology

Chiara Ambrosio

Introduction

Philosophers of science seem to have maintained a cautious distance from the practice of drawing. This is especially perplexing given the current revival of philosophical interest in scientific activities such as modelling and representing, which often incorporate drawings among their possible representational formats.[1] In this chapter, I want to invite philosophers of science to take drawing seriously – as a mode of visual inquiry in its own right and as an investigative practice aimed at producing a distinctively processual and dynamic kind of understanding.

Recent work across art, biology and process ontology (Anderson-Tempini et al. 2019) has begun to build a visual epistemology of processes by bringing the practice of drawing, as a pathway to process thinking, back into the laboratory. The line of investigation I pursue here is an explicit attempt at joining forces with this emergent literature, and extending it in what I take to be a compatible philosophical direction. In particular, I want to frame drawing as a distinctively *pragmatist visual epistemology* in its own right: a mode of *inquiry*, performed with pencil or pen on paper, in which one formulates visual hypotheses and experiments with the possible consequences of adopting certain ideas or conceptions, or with the consequences of seeing phenomena in a certain way.

The chapter will proceed as follows. I will start by outlining the key pragmatist concepts that underpin my account. While much contemporary process ontology has (rightly!) positioned itself as a continuation of the pragmatist programme of Alfred North Whitehead, I aim to look into a less obvious, but equally rich pragmatist source: the scientist, pragmatist philosopher, logician and father of semiotics Charles Sanders Peirce.[2] Along with being a prolific writer, Peirce was a compulsive doodler and an advocate and enthusiastic user of diagrammatic representations. It is by looking at how he incorporated different kinds of drawings in some of his philosophical arguments that I will lay the pragmatist groundwork for my discussion. Central to Peircean pragmatism (and to all pragmatist epistemology after Peirce) is the concept of *inquiry*: a fallible process of knowledge-seeking (Legg and Hookway 2021), which should take us from a state of doubt to a state of temporarily settled belief. While terms such as 'doubt' and 'belief' might suggest a theoretical, or even purely propositional characterization of inquiry, pragmatist scholars have repeatedly emphasized its practical dimension: 'When we inquire' Christopher Hookway has pointed out, 'we engage in a goal-directed activity; inquiry is a kind of action' (Hookway 2012: 40).

Building on Peirce's formulation, in the second part of this chapter, I present three ways in which drawing can be framed as a kind of visual inquiry and as a pragmatist visual epistemology in its own right: *delineating*, *reconfiguring* and *structuring*. Each of these three possible 'visual modes' of inquiry is supported by case studies of drawing in action, in a concrete scientific context. The use of the gerund (the suffix -ing) in the descriptions of these three modes of visual inquiry is deliberate: in all three cases, it aims at characterizing drawing (incidentally both a gerund and a noun!) first and foremost as a goal-oriented, epistemic *activity*.

Dot diagrams and serpentine lines: A pragmatist visual epistemology

'Though I draw incessantly, I have never drawn a prize' (L 387),[3] Peirce humorously confessed to his friend and supporter judge Francis C. Russell in an undated letter, probably written in the early months of 1896. This quote, and the mania for doodling and drawing it professes (see for example Figures 2.1 and 2.2), is increasingly attracting the interest of Peirce scholars as well as historians of art.[4] 'I do not think I ever reflect in words', he reminisced a few years later, in an equally well-known passage, 'I employ visual diagrams firstly because this way of thinking is my natural language of self-communion, and secondly because I am convinced that it is the best system for the purpose' (R 619: 8, 1909). Ranging from informal doodles to systematic diagrams,[5] Peirce's drawings offer a distinctively pragmatist visual counterpart to his philosophical arguments. In this section, I aim to reconstruct a pragmatist visual epistemology precisely from the philosophical use that Peirce makes of drawings and diagrams and show that they form a coherent line of inquiry in their own right – one that runs parallel to his formal philosophical arguments. Along with offering the conceptual and philosophical underpinning for the analysis that follows, I want to show that Peirce *practiced* philosophy

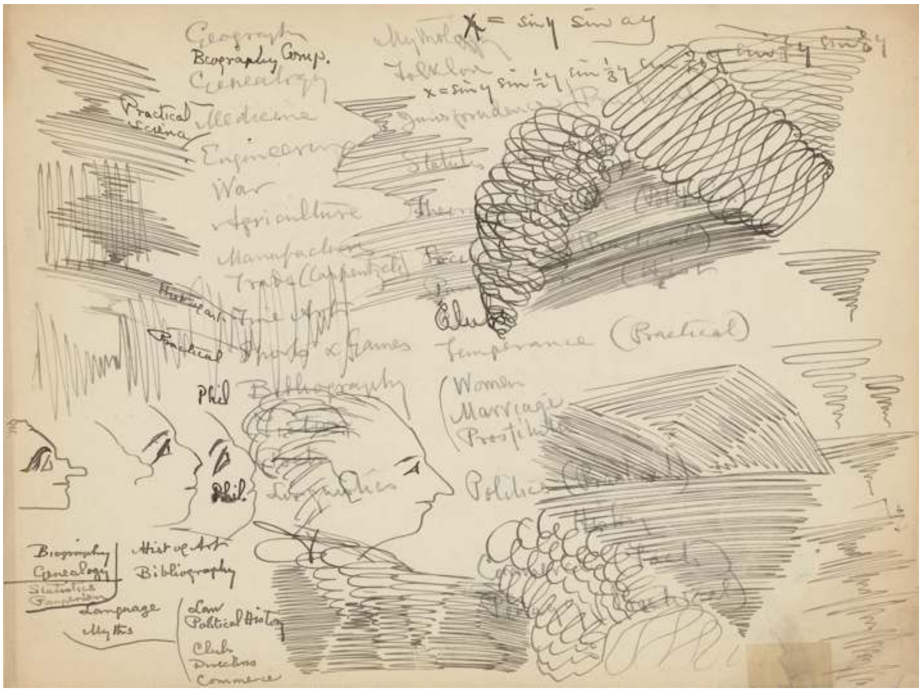


FIGURE 2.1: Charles S. Peirce, *Caricatures, Doodles, Drawings, Pen Trials*, autograph manuscript [MS Am 1632 (1538)], undated. Houghton Library, Harvard University.

through drawing and that his drawing practices are more than mere illustrations of his arguments: they are a way of experimenting, on paper (or on other media, as we will see later in this section), with the consequences of adopting particular conceptions.

My starting point is Peirce's 'How to make our ideas clear', an article published in 1878 in *Popular Science Monthly*. The article was part of a series collectively titled 'Illustrations of the Logic of Science'.[6] In the chapter, Peirce put forward what would later be labelled[7] as the pragmatic maxim:

> Consider what effects, which might conceivably have practical bearings, we conceive the object of our conception to have. Then, our conception of these effects is the whole of our conception of the object.
>
> (EP1, 132)[8]

In its original formulation, Pragmatism was born as a method to clarify the meaning of concepts or hypotheses by evaluating their 'practical bearings'. The maxim is part of an argument framed as a direct response to Descartes's 'clear and distinct ideas' and their legacy in logic (particularly in Leibniz). Peirce identified three levels or grades of clearness, which form our understanding of concepts. 'When

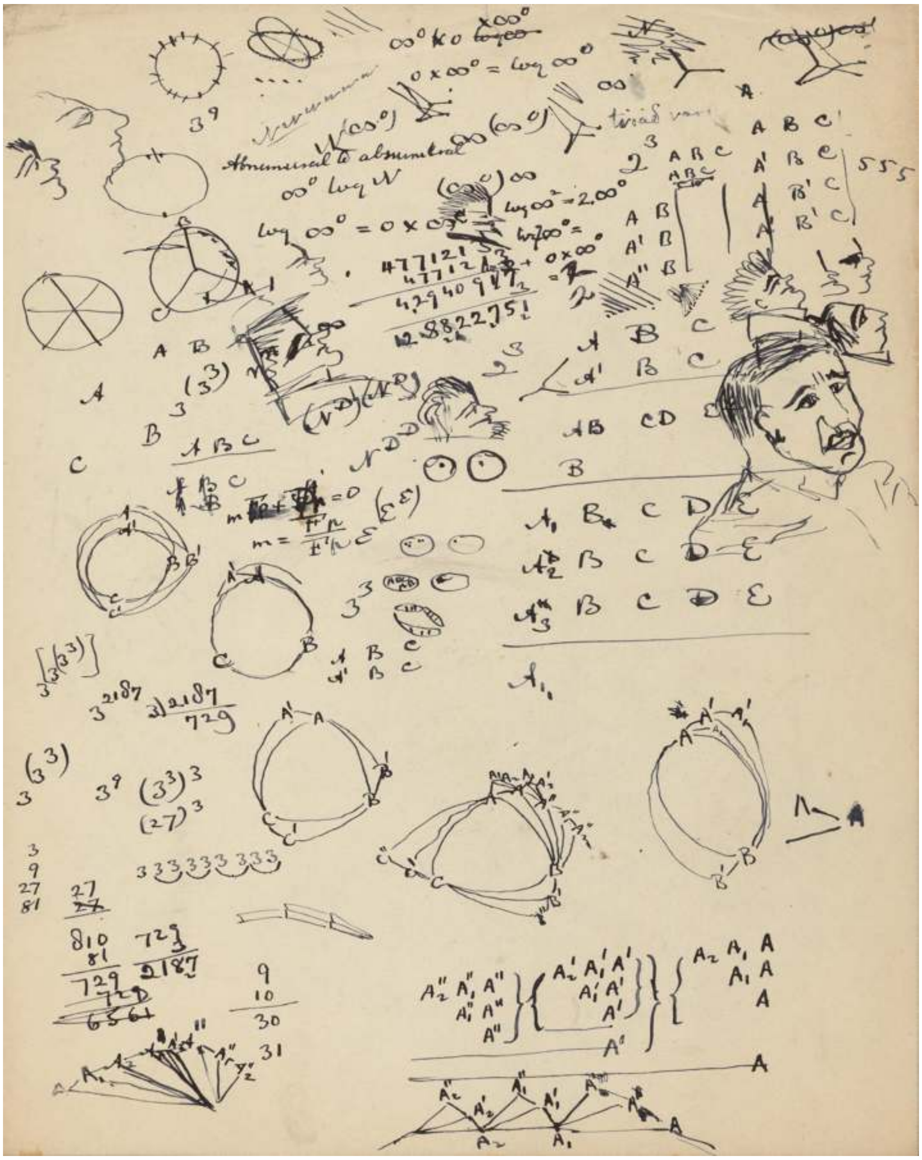


FIGURE 2.2: Charles S. Peirce, *Caricatures, Doodles, Drawings, Pen Trials*, autograph manuscript [MS Am 1632 (1538)], undated. Houghton Library, Harvard University.

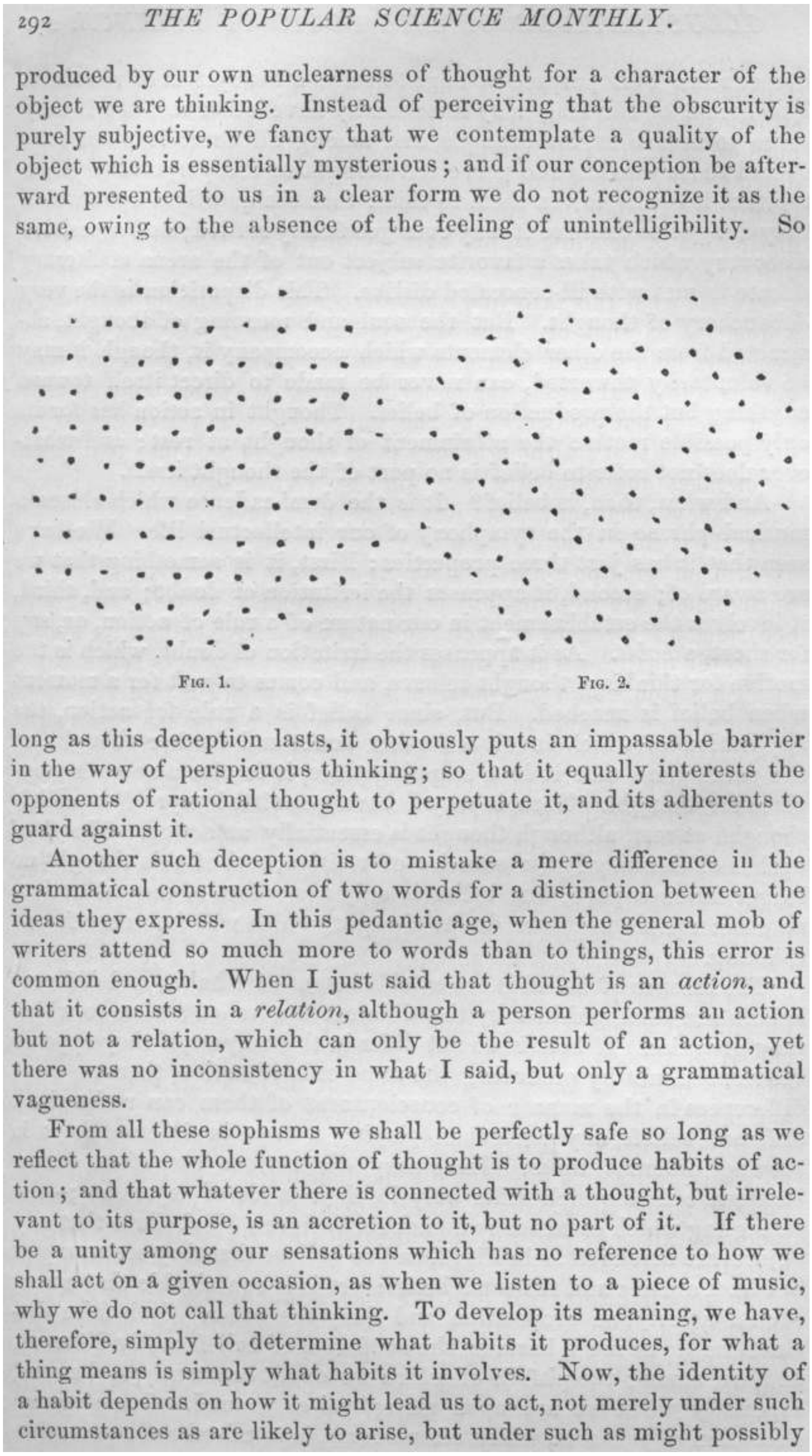
logicians speak of clearness', Peirce explains, 'they mean nothing more than … familiarity with an idea' (EP1, 125). This corresponds only to a very basic, first grade of clearness about the meaning of a concept – being able to identify instances of that concept in our ordinary experience. A second grade of clearness involves the supplement of distinctness: an idea is distinctly apprehended when we can define it in abstract terms. 'Here the logicians leave the subject', Peirce complains, 'and I would not have troubled the reader with what they have to say, if it were not such a striking example of how they have been slumbering through ages of intellectual activity' (EP1, 125). While becoming acquainted with an idea and analyzing definitions are important steps in coming to understand concepts, Peirce points out that they are limited on their own. The pragmatic maxim encapsulates a third, richer grade of clearness of apprehension of a concept: in a way that clearly betrays Peirce's scientific training, the maxim is an invitation to *experiment* with the consequences that would follow from adopting certain conceptions, hypotheses or states of affair.

In order to further ground the maxim, Peirce connects it to another central pragmatist insight: *inquiry*.[9] In 'The Fixation of Belief', the very first article of the 'Illustrations' series, Peirce had defined inquiry as 'the struggle to attain a state of belief' caused by 'the irritation of doubt' (EP1, 114). Doubt and belief are different states of mind, which produce very different effects: where doubt is a wish to ask a question, belief is a rule of action, or a kind of *habit*: '[it] does not make us act at once, but puts us into such a condition that we shall behave in a certain way, when the condition arises' (EP1, 114). Thus inquiry is the process that takes us from doubt to belief, but Peirce is clear that belief is never permanently fixed: 'Since belief is a rule for action, the application of which involves further doubt and further thought, at the same time that it is a stopping-place, it is also a starting-place for thought' (EP1, 129).

In 'How to make our ideas clear', Peirce brings the distinction between doubt and belief right to the core of his pragmatist maxim – and he does so by resorting to an intriguing visual example. Different beliefs, he claims, can be distinguished by the different habits they produce, and if they appease the same doubt – if they answer the same question – by producing the same habit, they are essentially the same belief. Here Peirce pauses for a moment, to articulate this claim through an illustration (Figure 2.3). 'Imaginary distinctions', he states, 'are often drawn between beliefs which differ only in their mode of expression; – the wrangling which ensues is real enough however' (EP1, 130). Pointing to the two dotted geometrical figures in the illustration, he continues:

> To believe that any objects are arranged as in Fig. 1 [Figure 2.3], and to believe that they are arranged in Fig. 2 [Figure 2.3], are one and the same belief; yet it is conceivable that a man should assert one proposition and deny the other.
>
> (EP1, 130)

In its extreme visual simplicity, Peirce's dot diagram encapsulates – albeit in a very condensed form – some key aspects of the pragmatist outlook he is presenting in the text. The immediate use of the diagram seems to be to illustrate the claim that superficial differences in 'mode of expression' do not affect the meaning of beliefs.



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produced by our own unclearness of thought for a character of the object we are thinking. Instead of perceiving that the obscurity is purely subjective, we fancy that we contemplate a quality of the object which is essentially mysterious; and if our conception be afterward presented to us in a clear form we do not recognize it as the same, owing to the absence of the feeling of unintelligibility. So

Fig. 1. Fig. 2.

long as this deception lasts, it obviously puts an impassable barrier in the way of perspicuous thinking; so that it equally interests the opponents of rational thought to perpetuate it, and its adherents to guard against it.

Another such deception is to mistake a mere difference in the grammatical construction of two words for a distinction between the ideas they express. In this pedantic age, when the general mob of writers attend so much more to words than to things, this error is common enough. When I just said that thought is an *action*, and that it consists in a *relation*, although a person performs an action but not a relation, which can only be the result of an action, yet there was no inconsistency in what I said, but only a grammatical vagueness.

From all these sophisms we shall be perfectly safe so long as we reflect that the whole function of thought is to produce habits of action; and that whatever there is connected with a thought, but irrelevant to its purpose, is an accretion to it, but no part of it. If there be a unity among our sensations which has no reference to how we shall act on a given occasion, as when we listen to a piece of music, why we do not call that thinking. To develop its meaning, we have, therefore, simply to determine what habits it produces, for what a thing means is simply what habits it involves. Now, the identity of a habit depends on how it might lead us to act, not merely under such circumstances as are likely to arise, but under such as might possibly

FIGURE 2.3: Charles Sanders Peirce, ‘How to make our ideas clear’, *Popular Science Monthly*, 12 (1878), p. 292. Ernst Mayr Library of the Museum of Comparative Zoology, Harvard University.

Indeed, a close look shows that the two dotted figures are one and the same – the only difference being that the figure on the right has been turned 45°. In a perceptive analysis of Peirce's diagram, Sarah Mirseyedi (2017) has highlighted a tension between the diagram's visual logic and the point Peirce is advancing in the text: 'the diagram remains stubbornly visual and technical', she observes, 'it makes plain the real sensation of visual discrepancy at the same time as its function in the text is meant to deny such discrepancy as a useful criterion in the judgment of conceptual clarity' (Mirseyedi 2017: 293). But this visual discrepancy fulfils precisely a pragmatist goal – and it does so in a counterintuitive way that is typical of Peirce's argumentative strategies. The conclusion that the two figures are the same is in fact reached through a process of pragmatic clarification: the identity between the two figures is 'discovered' by mentally tilting the figure on the right by 45°, superimposing the two figures and drawing the consequences of this mental operation. Thus, paradoxically, the realization that the differences in the two figures' modes of expression are *inconsequential* is reached precisely by pragmatically experimenting with the *consequences* of manipulating them.

The strategy of 'experimenting' – in this distinctive pragmatist sense – through the concrete and material manipulation of diagrams and drawings is ubiquitous in Peirce's writings. When it comes to diagrammatic representations, this pragmatist approach is characteristic of his broader, anti-positivistic account of the relationship between mathematics, philosophy and the sciences. As Peirce scholar Carolyn Eisele has persuasively argued, at the core of what Peirce dubbed his *exact philosophy* is a distinctively diagrammatic conception of mathematical reasoning:

> If one stops to examine the operation of this procedural mechanism in the 'proof' of a theorem from high school geometry, one would:
>
> 1. Construct an icon, the relation of whose parts is determined by the premises;
> 2. Experiment upon the effects of modifying this diagram. The probable modification is a construction;
> 3. Observe in this experiment certain relations between parts of the enlarged diagram over and above those which sufficed to determine its construction;
> 4. Satisfy oneself by inductive reasoning that these new relationships would always subsist where those in the premises existed.
>
> (HP1, 11)[10]

But even in the case of less strictly codified visual representations, this sense of 'experimenting' upon the effects of adopting, manipulating, or modifying the components of a drawing remains conceptually and practically crucial for Peirce – and indeed it serves as a bridge between these different modes of visual reasoning.

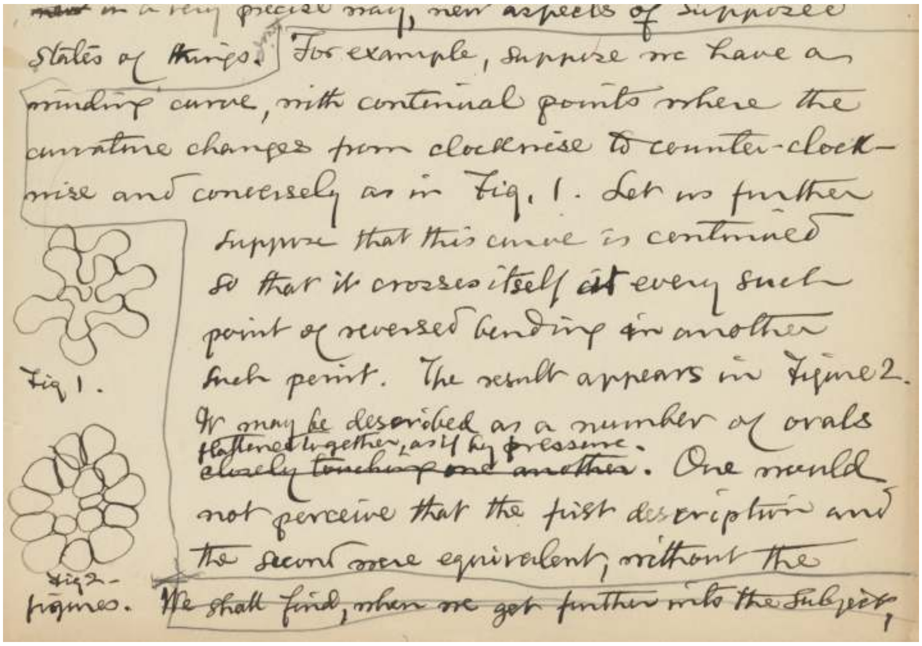
For example, in a prospective (but never published) book chapter titled 'What is a Sign?' (1893–95), Peirce explicitly brings together examples of drawing from art and science to give a pragmatist twist to his semiotic concept of iconicity. In a move that generated much philosophical debate (and which was partly responsible for many mischaracterizations of Peirce's account of iconicity in the twentieth century, and sadly beyond),[11] Peirce characterizes iconic signs as signs that exhibit a similarity or 'likeness' with the objects they stand for. But he is quick to clarify that the sense in which he uses 'likeness' goes beyond a mere similarity of appearances:

> Another example of likeness is the design an artist draws of a statue, pictorial composition or architectural elevation, or piece of decoration, by the contemplation of which he can ascertain whether what he proposes will be beautiful or satisfactory. The question asked is thus answered almost with certainty because it relates to how the artist will himself be affected. The reasoning of mathematicians will be found to turn chiefly upon the use of likenesses, which are the very hinges of the gates of their science. The utility of likenesses to mathematicians consists in their suggesting, in a very precise way, new aspects of supposed states of things.
>
> (EP2, 6)

Far from a point-to-point correspondence, here 'likeness' for Peirce has a distinctively generative dimension: the process of constructing a drawing or diagram, and considering the consequences of that construction, allows the artist, architect and mathematician to discover something new about the object of their construction, precisely through the manipulation of their respective representations. This characterization of likeness is immediately followed by an example, in which Peirce, once again, invites his readers to engage in a visual experiment (see Figure 2.4):

> Suppose we have a winding curve, with continual points where the curvature changes from clockwise to counter-clockwise and conversely, as in figure 1 [Figure 2.4]. Let us further suppose that this curve is continued so that it crosses itself at every such point of reversed bending in another such point. The result appears in figure 2 [Figure 2.4]. It may be described as a number of ovals flattened together, as if by pressure. One would not perceive that the first description and the second were equivalent without the figures.
>
> (EP2, 6)

Moving from dots to lines, Peirce here shows that a relation of equivalence between the two figures can be visually inferred – in a way that would not have been otherwise – by reference to the images. Where in his 1878 dot diagram, Peirce asks his readers



~~[illegible]~~ in a very precise way, new aspects of supposed states of things. For example, suppose we have a winding curve, with continual points where the curvature changes from clockwise to counter-clockwise and conversely as in Fig. 1. Let us further suppose that this curve is continued so that it crosses itself at every such point of reversed bending in another such point. The result appears in Figure 2. It may be described as a number of ovals flattened together, as if by pressure. ~~closely touching one another~~. One would not perceive that the first description and the second were equivalent, without the figures. ~~We shall find, when we get further into the subject,~~

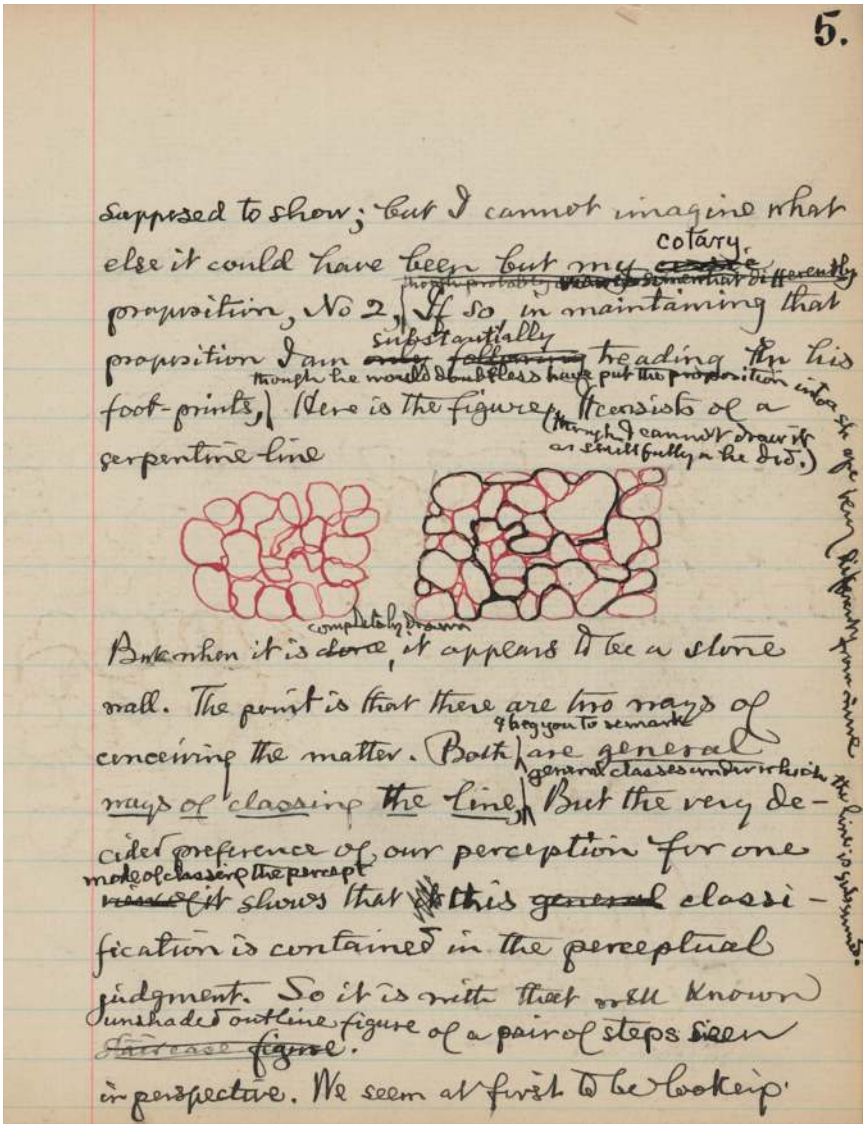
Fig 1.

Fig 2.

FIGURE 2.4: Charles S. Peirce, MS 404, ‘The Art of Reasoning’ (1893–95), p. 36 (detail). The Houghton Library, Harvard University.

to rotate one of the two figures and superimpose it on the other, here he invites them to ‘follow the line’. Re-enacting the process of experimenting with the curve – re-drawing the winding line as in the figure at the top, closing each loop as in the figure below it – leads to the visual discovery that the two figures are one the continuation of the other. A visual experiment at the boundary between a doodle and a diagram, Peirce’s winding lines deliberately create perplexity at first – only to compel the viewer/interpreter of the drawing to act on that perplexity by retracing his initial marks on the page and reimagining the construction of his experiment.

Peirce’s winding lines reappear a few years later (Figure 2.5), in the context of a series of lectures he delivered in Harvard in 1903. In direct response to William James’s request to offer a course on Pragmatism, Peirce prepared seven lectures, in which he revisited his pragmatist writings of the late 1870s and grounded his version of Pragmatism in other key pillars of his philosophy: his phenomenology and theory of the categories, his account of the normative sciences, his account of abduction, and – key to the use he makes of the drawing in question – his theory of perception. As Tullio Viola (2012) has noted, the manuscripts of Peirce’s ‘Harvard Lectures on Pragmatism’ are among the texts in which he uses drawing in a most extensive way ‘and in a manner that is tightly related to the argument’s development’ (Viola 2012: 117). Prepared as texts to be read to an audience, the drawings in the manuscripts would be reproduced on a blackboard



5.

supposed to show; but I cannot imagine what else it could have been but my ~~[illegible]~~ cotary ~~though probably [illegible] somewhat differently~~ proposition, No 2, [If so in maintaining that proposition I am ~~only~~ substantially ~~following~~ treading in his though he would doubtless have put the proposition into [illegible] very differently from mine foot-prints,] (Here is the figure, (though I cannot draw it as skillfully as he did.) It consists of a serpentine line

But when it is ~~done~~ completely drawn, it appears to be a stone wall. The point is that there are two ways of conceiving the matter. (Both & beg you to remark are general ways of classing the line, general classes under which the line is subsumed.) But the very decided preference of our perception for one mode of classing the percept ~~[illegible] of~~ ~~it~~ shows that ~~[illegible]~~ this ~~general~~ classification is contained in the perceptual judgment. So it is with that well known ~~staircase figure~~ unshaded outline figure of a pair of steps seen in perspective. We seem at first to be looking

FIGURE 2.5: Charles Sanders Peirce, MS 315, ‘Harvard Lectures on Pragmatism’, Lecture VII (1903: 5). The Houghton Library, Harvard University.

or as magic lantern slides, giving us a glimpse of the performative aspect of Peirce’s lectures.

This performative aspect comes through specifically in the seventh and final Harvard Lecture, where the drawing in Figure 2.5 appears. Here Peirce presents three ‘*cotary* propositions’ (from *cōs*, *cōtis*, ‘whetstone’), which he claims will ‘put an edge on the maxim of pragmatism’ (EP2, 226). Adopting a scholastic idea of Aristotelian legacy, Peirce presents his first cotary proposition as ‘*nihil est in intellectu quin prius fuerit in sensu*’ (‘nothing is in the intellect which was not previously in the senses'). Translated in pragmatist terms, the proposition crucially links meaning, perception and experience: the meaning (*intellectus*) of any idea or cognition is grounded in our perceptual judgments (*in sensu*). Peirce's second cotary proposition states that perceptual judgments contain general elements: perception is not a private matter – our perceptual judgments can be intersubjectively shared, evaluated and exposed to the scrutiny of a community of inquirers. Lastly, Peirce's third cotary proposition contains an extremely rich – and extremely dense – version of his account of the hypothetical nature of perception: 'abductive inference shades into perceptual judgments without any sharp line of demarcation between them' (EP2, 227). Perceptual judgments, he claims, are but extreme cases of abductive inference.

It is the relationship between Peirce's second and third cotary propositions that the drawing in Figure 2.5 elucidates. In the course of his lecture, Peirce would have turned to the blackboard to draw it, while explaining:

> I will show you a figure which I remember my father drawing in one of his lectures. I do not remember what it was supposed to show; but I cannot imagine what else it could have been but my cotary proposition number two […]. Here is the figure (though I cannot draw it as skilfully as he did). It consists of a serpentine line. But when it is completely drawn, it appears to be a stone wall. The point is that there are two ways of conceiving the matter. Both, I beg you to remark, are *general* ways of classing the line, *general classes* under which the line can be subsumed. But the very decided preference for one mode of classing the percept shows that this classification is contained in the perceptual judgment.
>
> (Peirce EP2, 228, emphasis added)

Peirce's description of the drawing as a 'serpentine line' points directly to William Hogarth's 1753 *Analysis of Beauty*, and as Viola (2012: 132–33) has insightfully demonstrated, it resonates with another intriguing detail in the passage: the reference to Peirce's father, the Harvard mathematician and astronomer Benjamin Peirce. Hogarth saw the serpentine line as bringing about continuity and movement to the otherwise discrete impressions we receive from the senses; Benjamin Peirce is likely to have used it in his lectures to make an analogous point about the continuity of time.[12] In his 1903 lecture, Peirce brings these two approaches – and the aesthetic and scientific traditions they embody – together, in an account of the continuous nature of perceptual experience, which he considers indispensable to give 'an edge' to his mature Pragmatism. By actively performing the drawing of the line on a blackboard, Peirce invites his audience, once again, to partake in a pragmatist visual experiment – this time by considering the consequences of adopting a particular perceptual hypothesis. As the audience saw him beginning to draw, they would interpret the marks on the board as a winding line. But as Peirce closed each loop, they would see the line *as* a stone wall. Both ways of experiencing the drawings, Peirce claims, are *general* ways of classing the marks on the board: they are fallible *judgments* that are continuous with the supposedly 'factual' core of perceptual experience (what Peirce calls 'the percept' in the quote). However cumbersome it might read at first, Peirce's theory of perception merges two important complementary insights: that we experience what is external to us (the marks on the board, in this case) somewhat 'immediately', but also that those direct experiences, woven into *general* judgments (classing the line *as* a stone wall), are intersubjectively shareable and evaluable. As Cathy Legg (2017) has pointed out, this is well captured by Peirce's slogan that 'nothing at all ... is absolutely confrontitial', but at the same time 'the confrontitial is continually flowing in upon us' (CP 7.653;[13] cf. Legg 2017: 44ff).

In all three examples I showed above, Peirce used drawing in accordance with his pragmatic maxim – as a form of philosophical inquiry in its own right, as a means of pragmatic clarification, and as a way of experimenting, with pen on paper or chalk on a blackboard, with the consequences of adopting certain ideas or conceptions. In later years, drawing also added a further dimension to the pragmatic maxim: it afforded Peirce the opportunity to probe the boundaries between conceptions and perceptions, firmly grounding his Pragmatism in the realm of experience. This Peircean approach to drawing, illustrated via Peirce's own visual inquiries, forms the core of what I have called a *pragmatist visual epistemology*.

In what follows, I will present three examples that will further define how drawing can serve as a mode of inquiry and as an experimental practice, in the Peircean sense I began sketching in this section. But while inquiry and experiment are the pragmatist common traits to all three of my case studies, here I want to add the important qualification that different *aims* importantly shape the direction inquiry might take – and this qualification has repercussions on how pragmatically we think about inquiry through drawing. This is why the examples below are three (but they could be more!) – in that they pick out different ways in which formulating visual hypotheses and considering their consequences is directed to the fulfilment of a particular *aim*.[14] This will allow me to align different kinds or 'modes' of visual inquiries to different aspects of the pragmatist visual epistemology I outlined above. Thus, Peirce's account of the continuous nature of perception, its generality and its hypothetical nature will become paramount in the case of observational drawing, as exemplified by the mode of inquiry that I call *delineating*. Peirce's invitation to consider our beliefs and habits only as provisionally 'fixed' finds a counterpart in the practice that I describe below as *reconfiguring*, whereby, through drawing, doubt is deliberately built into the production of alternative representations and understandings of purportedly 'established' phenomena. Lastly, a pragmatist outlook will challenge even what is commonly taken to be as 'static' structure. In my third and final case study, I will advocate a pragmatic and dynamic account of *structuring* as a process where aspectual features are selectively made visible and manipulated for the purposes of classification. All three cases present different and complementary ways in which drawing qualifies as a visual epistemology in a pragmatist sense: a dynamic, goal-oriented activity; a set of actions which invite further action towards the fulfilment of specific aims.

Delineating

My first example of drawing as a pragmatist visual epistemology is *delineating*, a category I borrow directly from the work of medical artist and researcher Lucy Lyons (Lyons 2009, 2012, 2017; Figure 2.6).[15] Lyons developed the method of delineation as an observational and phenomenological inquiry, carried out through drawing, into a rare pathological condition known as *fibrodysplasia ossificans progressiva*, in which connective tissue turns into bone. From a conceptual and historiographical point of view, Lyons inscribes her practice in a broader tradition at the intersections between drawing and medicine, inaugurated by the nineteenth-century British pathologist Robert Carswell. It was Carswell, Lyons point out, who first described his own illustrations as 'delineations' (Figure 2.7), qualifying them as follows:

> You should see these Delineations [...] you may appreciate their value not as art, but as instruments of medical science by means of which *more precise, more accurate and more perfect information may be acquired and communicated respecting the various and numerous organic changes to which the human body is subject*.
>
> (Carswell 1831, cited in Lyons 2009: 10, emphasis added)

Carswell's quote highlights three distinctive features of delineating, which in turn inform Lyons's approach. First, through delineation, drawing becomes 'an instrument of medical science': far from merely copying, this manner of observational drawing has a distinctively exploratory dimension. Second, this exploratory dimension brings about an enriched, 'more perfect', understanding of the object under investigation. Lastly, delineating does not amount to capturing static objects: it aims at revealing, dynamically, 'the numerous organic changes to which the body is subject'. Lyons explains this aspect of delineation by pointing out that, rather than objects per se, delineation aims to offer a glimpse of multiple, unique encounters with particular features of *fibrodysplasia ossificans progressiva*.

The foil of Lyons's practice is automated medical imaging, particularly photography.[16] In an account of her early steps into researching *fibrodysplasia*

FIGURE 2.6: Lucy Lyons, *Delineation 16 Basel 191 Side View*, graphite pencil on paper, 297 × 420 mm (2016). © Lucy Lyons. Reproduced with the artist's permission.

ossificans progressiva, she recalls the confusion generated by trying to discern sites of bone growth from simply looking at photographs of the conditions:

> I could not understand what I was seeing until I began to 'draw my way into understanding it'; drawing the details, realizing things were not how they seemed and spending time visually unpicking and attempting to understand what I was encountering. The confusion of excess bone was visually difficult to interpret, more

FIGURE 2.7: Robert Carswell, *Case of Richard Smith. Dr Walsh's Case Books U.C.H.*, 1832, vol. VII Males p. 172. UCL Library Services Special Collections CARSWELL/I/879.

> so when presented as a photograph as everything becomes flattened and tonally similar.
>
> (Lyons 2012: 3)

This passage is revealing in many ways. In an immediate sense, 'drawing one's way into understanding' is a way of bringing clarity in the confusion of a condition that remains poorly studied, and that mechanical reproduction, in its purported 'faithfulness' to every single detail, only contributes to obscure further. It is important to specify that photographs of the condition were only one of the many sources of Lyons's research. She primarily drew from actual bodies: preserved museum specimens, bodies of donors given to medical collections and being prepared for conservation but also living patients affected by the disease. To ensure detail and at the same time selectiveness, Lyons's method was strictly regimented: delineating consists in the use of simple materials – pencil lines on paper, with no added colour. In contrast with standard textbook or atlas images, Lyons's drawings are not labelled, and, in several images, the multiple faded marks on the page betray false starts and stumbling blocks in the process of grasping relevant details. For example, referring to the multiple marks around the skull in *Delineation no. 15* (Figure 2.8), Lyons states that 'they are a record of the frequency I observed and had to re-adjust lines to more precisely convey the complexity and detail of the ossification that occurred' (Lyons 2009: 138).

Delineating as an activity involves the coordination of an ensemble of practices: focused observation ('slow looking', in Lyons's terminology; see Lyons 2017: 30ff),

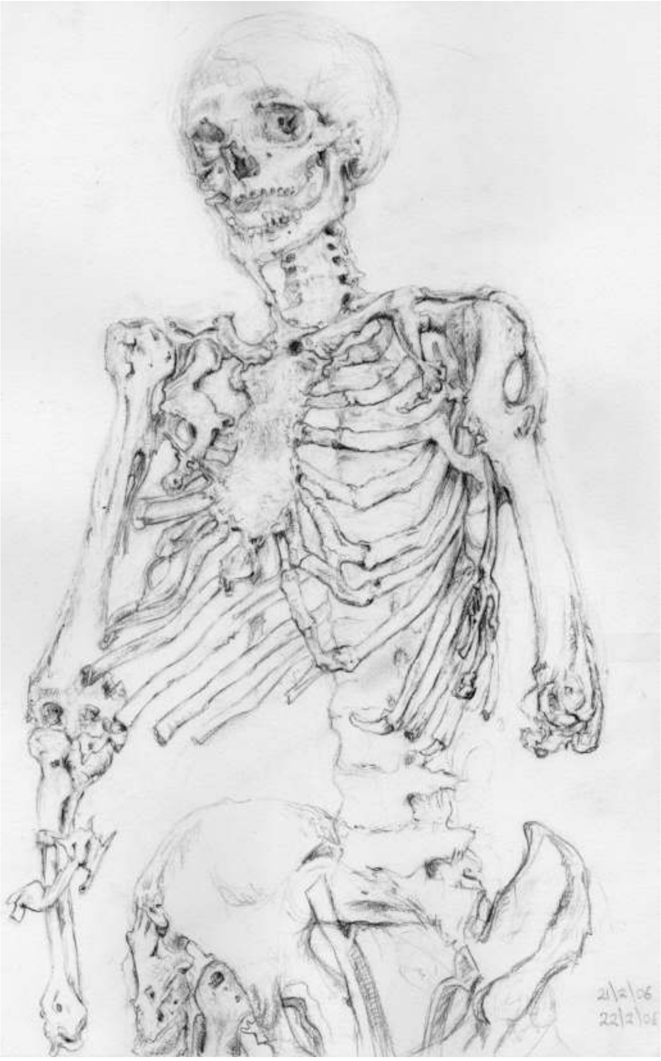


FIGURE 2.8: Lucy Lyons, *Delineation 15 2nd Basel 190 Front View B, graphite pencil on paper*, 297 × 420 mm (2016). © Lucy Lyons. Reproduced with the artist's permission.

selection and extraction of salient features, simplification through a realistic rendering. The process is also iterative, in that it moves from observation to drawing, to new observations and further corrections of the marks on paper: 'understanding of the visual experience', Lyons points out, 'is developed and fed back into the process of continuing to make marks' (Lyons 2009: 27). It is through this iterative ensemble of practices that bone configurations emerge on the page, and with them new modes of understanding *fibrodysplasia ossificans progressiva*: delineating is a way of bringing out, through intense observation and drawing, details of the condition that remain unobserved. Just like Peirce's stone wall, Lyons's lines are the materialization of a series of *hypotheses* about sites and patterns of ossification on the page, which are iteratively corrected as the drawing unfolds on paper in parallel with observation. The interactions with pathologists, alongside patients and museum curators, is also an indispensable aspect of the practice. Through delineation, for example, Lyons was able to draw pathologists' attention to specific sites and patterns of bone growth, otherwise indiscernible through a photographic rendering. Patients themselves gained a clearer understanding of their condition, expressing reactions that ranged from renewed awareness to shock for the extreme clarity through which the drawing disclosed what was happening to their bodies (Lyons 2009: 279–82). In this respect, delineating crucially mediates between aspects of the disease itself and the perspectives, experiences and knowledge of patients and pathologists.

Lyons points out that, as a practice and a process, delineation is inevitably *particular* (Lyons 2009: 94). As *fibrodysplasia ossificans progressiva* manifests differently in each patient, and as each encounter with aspects of the disease is unique, the drawings – just like the condition itself – seem to escape generalization. But while the phenomenological aspects of delineating pull Lyons's attention and practice towards the particular, I want to suggest that delineating displays at the same time a pragmatist dimension, which orients it towards achieving a very distinctive kind of *generality*. Here I use 'generality' in the Peircean sense I outlined in the previous section: as something that can be shared, made public and in principle challenged or questioned. Indeed, delineating importantly capitalizes on the very hypothetical nature of perception and experience. The marks on paper, including – perhaps *particularly* – those evidencing false starts and stumbling blocks, are themselves a series of perceptual hypotheses about the salient features of the phenomena under investigation. Through the activity of delineating, drawing becomes a means of articulating perceptual hypotheses about what is being observed, and making them public. The practice itself brings those hypotheses into a public arena, offering possible pathways towards clarifying confusion (around sites of bone growth, for example), and engaging medical practitioners, patients and museum curators in a collective conversation.

Reconfiguring

My second example comes from a project that forms the core of this edited collection: Gemma Anderson-Tempini, John Dupré and James Wakefield's proposal of bringing drawing back at the centre of cell biology. This line of investigation resonates with the renewed attention that philosophers of science are paying to visualization and representation in cell biology (Bechtel and Bolhagen 2019), but also with the historically sensitive, relational view of the cell 'as a nexus' recently proposed by Maureen O'Malley and Staffan Müller-Wille:

> The cell, we suggest, is a nexus: a connection point between disciplines, methods, technologies, concepts, structures and processes. Its importance to life, and to the life sciences and beyond, is because of this remarkable position as a nexus, and because of the cell's apparently inexhaustible potential to be found in such connective relationships.
>
> (O'Malley and Müller-Wille 2010: 169)

Anderson-Tempini et al. (2019; see also this volume) offer a detailed account, complete with supplementary documentation, of how drawing can contribute to reconfigure cell division as a process. They show that drawing offers an extremely powerful alternative to two recent tendencies in contemporary representations of mitosis. On the one hand, advanced imaging techniques impose a focus on *measuring* cell division and the processes involved in it, at the expenses of the kinds of questions that could arise if biologists focused on drawing what they observed. On the other hand, even more 'traditional', textbook representations of mitosis tend to focus on distinct, clear and separate stages of cell division, while playing down its nature of a process. 'One downside of the decline of drawing', Anderson-Tempini, Dupré and Wakefield argue, 'is that it has eliminated a degree of exploratory imagination – and, therefore, a source of new ideas and hypotheses – from the scientific process' (Anderson-Tempini et al. 2019: 1). Hidden between the lines of their appeal to a return to drawing is, I want to suggest, a pragmatist argument: the decline of drawing ultimately amounts to 'block[ing] the way of inquiry' (EP2, 48), to use a famous Peircean expression. In this section, I want to present the role of drawing in the context of Anderson-Tempini, Dupré and Wakefield's project as a case of *reconfiguring*,[17] which I frame in pragmatist terms as a way of 'drawing doubt into inquiry'. Where delineating consists in visually suggesting shareable hypotheses about unfamiliar objects and phenomena, *reconfiguring* openly challenges, through the adoption of a dynamic view, established modes of representing. It deliberately capitalizes on the introduction of alternatives in order to keep the way of inquiry open.

Conceived as a collaboration between an artist (Anderson-Tempini), a philosopher (Dupré) and a biologist (Wakefield), the project developed through a series of drawing labs in which, through drawing, biologists were explicitly invited to think philosophically about mitosis as a process. The way in which the collaboration unfolded is clearly revealing of a progressive – but also hard-won – departure from viewing mitosis along traditional, structure-based principles, and a gradual opening up towards a processual view. This transition took effort: the outputs of early drawing labs remained anchored to textbook representations, and even when the participants were explicitly invited to experiment with dynamic concepts, processes were rendered at best through arrows and labels, still very much along the lines of standard scientific illustrations.[18]

A turning point occurred with the introduction of concepts that fell outside the immediate realm of cell biology. Drawing on choreographic and musical principles, Anderson-Tempini began experimenting with the creation of a 3D ‘score’ (with time added as a fourth dimension) of mitosis (see Figure 5.6 in Chapter 5 in this collection):[19] a set of guides or clues to orchestrate the various components of cell division in a process unfolding as a polyphony through time. Note how the overall score explicitly aimed to challenge established representations: despite all phases of mitosis are clearly labelled and remain embedded in the drawing, the directionality and overall shape of the process looks – and to an extent *feels* – radically different.

In pragmatist terms, the introduction of the score was a first step towards unsettling established beliefs and the habits of action following from them. The intervention of the artist in the context of technical and extremely specialized studies of mitosis served to embed, right at the core of biological investigations of cell division, counterfactual questions such as ‘what would happen if we used continuous lines rather than self-contained illustrations of the stages of cell division?’ or ‘what would happen if we changed the directionality and shape of the overall process?’ It is in this sense that reconfiguring is a way of ‘drawing doubt into inquiry’: not an attempt at undermining the achievements of current research, but a prompt to consider the possible consequences of seeing and representing phenomena in a different way.

The introduction of the score marked a turning point in reconfiguring mitosis, from which radically new modes of representation followed. In line with Wakefield’s specialized research, new drawings focused on microtubules, which are responsible for the structure and shape of eukaryotic cells (see Figure 5.7 in Chapter 5 in this collection).[20] The drawings aimed to replace physical renderings of microtubules with a more ‘processual’ representation, with microtubule-generating pathways represented in different colours. Note that physical representations of chromosomes were retained, as the drawings – which are to be read vertically starting from the bottom – present their movement and interactions with microtubule-generating pathways through blue lines.

An interesting aspect of this stage of the research is the productive 'confusion' these images generated. As Anderson-Tempini, Dupré and Wakefield note, by this point, participants almost no longer knew what they were seeing through the drawings:

> At the time of drawing […] it was unclear what the overall sculpted shape related to, besides somehow including a dynamic perspective on the organisation of microtubules. A series of conversations among the whole team helped to define the overall changing shape of the image as being related to the energy inherent in the microtubule system(s) over time. This key reflection allowed the same principle to be applied to the chromosomes.
>
> (Anderson-Tempini et al. 2019: 6)

While 'liberating' cell division from the restraints of static, sequential and self-contained stages of representation, the score also created a pause for doubt. But this moment of hesitation served as a materialization on the page of the very dynamics of inquiry, again in the Peircean sense I outlined in the first part of this chapter. By deliberately disturbing established beliefs, the confusion introduced by the score prompted a process of collective, pragmatic clarification. Considering the consequences of adopting the hypothesis that the changing image in the drawing may be related to the energy of the microtubules system over time, allowed the team to extend the same principle to a processual representation of chromosomes, and eventually set into motion, through a new series of drawings, the overall process of mitosis (see Figure 5.13 in Chapter 5 in this collection).[21]

In this final series of drawings 'everything flows', to borrow the slogan of Heraclitean origin adopted by Dupré and Nicholson (2018) in their process ontology. Dynamic lines in unconventional colours set the various processes involved in cell division into motion: yellow for chromosome-related processes, purple for the energy related to the input of microtubules pathways, brown for activities in the cell cortex. 'Finally', Anderson-Tempini, Dupré and Wakefield sum up, 'by adding all the shapes together to form an overall outline, a full representation of the total process of cell division was generated' (Anderson-Tempini et al. 2019: 6).

As part of a pragmatist visual epistemology, reconfiguring has a distinctive generative dimension. Anderson-Tempini, Dupré and Wakefield's study has shown how drawing can be actively deployed to probe established modes of representation, suggesting alternative ways of framing research questions and thus opening new paths of inquiry. Indeed, alongside 'setting into motion' a process that had been frozen into textbooks as a sequence of static snapshots, reconfiguring prompted researchers to ask further questions about what would happen if other elements and systems involved in mitosis were incorporated in the drawing, and how would drawing help gauge the relationships between these components in greater detail (Anderson-Tempini et al. 2019: 6). The process generated questions for art practice as well, particularly on how drawing could effectively capture interactions and processes within processes in a way that would continue to generate interesting scientific questions. And lastly, by 'drawing doubt into inquiry' reconfiguring disclosed important – and unforeseen – methodological insights about the processual nature of the research itself, which emerged through a reflection on the very relationship that practitioners establish with their visual displays. Anderson-Tempini, Dupré and Wakefield conclude: 'drawing shifts the focus from the image as product (an almost inevitable consequence of merely witnessing biological processes through various imaging devices) to the production of the image as an integral part of research' (Anderson-Tempini et al. 2019: 8). Thus, the dynamics of doubt and belief – and their visual materializations and reconfigurations on the page – shape the course of research as well as the very identities of the practitioners that partake in it.

Structuring

Jane Richardson's famous ribbon drawings of proteins (Figure 2.9) form the last of my case studies. In this third and final section, I want to examine Richardson's

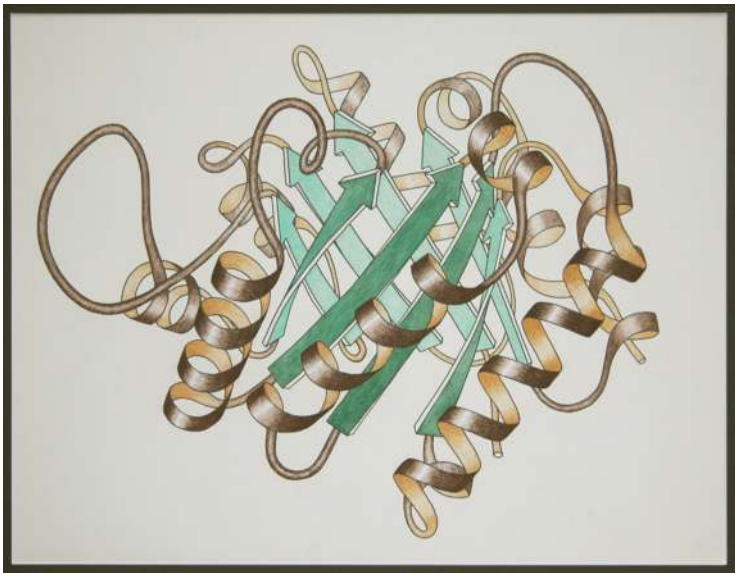


FIGURE 2.9: Jane Richardson, *Ribbon schematic of the 3D structure of the protein triose phosphate isomerase*, hand drawn and coloured (1981). CC BY 3.0 https://creativecommons.org/licenses/by/3.0/legalcode.

protein drawings as examples of *structuring*: the activity of making patterns and relations visible, for the purpose of comparison and classification. In Richardson's own words: 'making a drawing can change one's scientific understanding of a protein, sometimes revealing a preferable classification' (Richardson 2000: 624). I want to suggest that *structuring* resonates with two key aspects of the pragmatist visual epistemology I am proposing in this chapter. In stark contrast with the idea of (static) permanence and objective invariance often associated with structural talk in philosophy, *structuring* through drawing involves first and foremost decisions and choices, aimed to facilitate the selection and manipulation of relevant features. Second – and immediately following from the quote above – these choices, and the evaluation of their consequences, also fulfil the important goal of rendering visual inquiries into structural features *communicable* across a scientific community. I will return to this important point below.

First published in 1981 in a landmark paper in structural biology titled 'The anatomy and taxonomy of protein structure' (Richardson 1981), Richardson's drawings remain only marginally discussed in historical and philosophical accounts of protein research. One important exception is Bruno Strasser (2012, 2019), who helpfully shows how Richardson's taxonomical approach to protein structure clashes with, and contributes to challenge, established narratives of molecular biology as paradigmatic of twentieth-century experimentalism.[22] Instead, Strasser argues, Richardson's approach aligns with traditions of collecting, comparing and classifying that are distinctive of natural history (Strasser 2019: 332). He notes that Richardson acknowledged this lineage explicitly in her original study of the anatomy and taxonomy of protein structure:

> The vast accumulation of information about protein structures provides a fresh opportunity to do *descriptive natural history*, as though we had been presented with the tropical jungles of a totally new planet. It is in the spirit of this *new natural history* that we will attempt to investigate the anatomy and taxonomy of protein structures.
>
> (Richardson 1981: 170, emphasis added; cf. also Strasser 2019: 333)

Originally based on molecular patterns produced through X-ray crystallography, Richardson's drawings departed from the complexity of atomic models[23] and followed instead her insight that pattern similarities among protein structures can be due to folding preferences. At a time of taxonomical confusion in the field, they answered, visually, the important question of whether proteins exhibit any regularities in their structures. The drawings are often praised for their elegance, alongside their taxonomical effectiveness: spiral ribbons stand in for alpha helices, rounded ropes for molecular 'loops', and smoothed arrows (with added thickness to emphasize their orientation) for beta-strands. Importantly, as is evident from Figure 2.9, they are drawn in perspective.

Commenting on the elements that form the design of her drawings, Richardson noted: ‘Surprisingly, these disparate parts look visually unified and intelligible’ (Richardson 2000: 624). It is both remarkable and refreshing to read Richardson’s description of the sense of unity and intelligibility arising from her drawings as ‘surprising’ – and indeed unity and intelligibility are themselves surprising achievements of the process of structuring enabled by the drawings. Moreover, structuring, classification and intelligibility are all intertwined in Richardson’s method: after grouping proteins into classes according to their structures, the drawings provided a simplified visual system that would make their common structural features *evident*. In pragmatist terms, far from ‘fixing’ structure permanently, the ribbon drawings approach it dynamically and selectively, inviting the viewer/user of the representation to consider the consequences of seeing and grouping salient features in a certain way.

In one of the few available philosophical studies addressing Richardson’s drawings, Grant Fisher (2016) qualifies them as a clear case of representations in which the choice of a particular design has epistemic consequences in its own right. Drawing on Lopes (1996), he argues that the aim of Richardson’s drawings is to ‘manipulate aspectual structure’ (Fisher 2017: 26): structural ‘motifs’ emerge from the drawings selectively and relationally, through the design’s ability to capture salient taxonomical features. This connects with the perspectival rendering of the drawings, which are clearly not perspectival in any ‘optical’ sense (there is no concrete object drawn from a specific point of view behind the drawings). Instead, perspective here partakes of the selective nature of the design and, in combination with the simple visual system of ribbons, ropes, and arrows, allows the viewers/users of the diagrams ‘to gain control over what is and what is not represented’ (Fisher 2017: 26).

Richardson’s use of drawings was not uncontroversial. As Strasser (2019: 178ff) notes, protein taxonomists in Richardson’s time developed automated methods that would analyze ‘objectively’ the structure and coordinates of proteins and identify protein domains. Adopting a rhetoric of ‘mechanical objectivity’ (Daston and Galison 2007), they explicitly pitted automated methods against the inevitably subjective nature of drawing, adding the reason that drawing would bring as many criteria in the field of protein research and classification as there would be researchers (Strasser 2019: 179). Richardson seems to have been well aware of this criticism and addressed it in more than one of her publications. For example, in a 2000 *Nature* article that traces the history of her early ribbon drawings, she observes:

> Ribbon drawings are an excellent tool for first comprehending the overall organization of a protein structure, on which one can later hang the important details.

> *Decisions about representation, secondary structure, and viewpoint, whether done by hand or by a computer algorithm, are inherently arbitrary and subjective but also serve to communicate ideas about which structural aspects are important.*
>
> (Richardson 2000: 625, emphasis added)

Structuring proteins involves judgment. In Richardson's case, the goal was to facilitate comparison through the deliberate manipulation of structural features, for the purposes of classification. Thus, she argues, judgments about which aspects could be left out, as well as what to include in the design will be *inevitably* subjective – even when they are embedded in an automated process. Indeed, in an earlier article, Richardson explicitly adopted a pluralistic attitude towards different methods of 'looking at proteins', which explicitly emphasized *communicability*:

> Much of what we have discussed about types of representations is directed toward the researcher trying to find new, significant relationships in a protein structure. *But a second, especially crucial role of models, drawings, and computer graphics is to make explicit a relationship that you have found, enabling other people to see it as well.* This often can be done just by making the relevant part a heavier line or a brighter color, or by deleting most of everything else, but it always requires explicit effort. *The total process of looking scientifically at proteins involves communication as well as perception.*
>
> (Richardson et al. 1992: 1189, emphasis added)

Inscribing her drawings in the far broader array of modelling techniques in structural and molecular biology, Richardson here is making a claim for the continuity and complementarity of different methods. She is also responding to her critics by pointing out that different techniques, including her own, will disclose different 'aspectual' features of protein structure. The common trait among all these modelling methods is precisely *not* to freeze structure in time, but to show how different *structuring judgments* dynamically disclose relevant features, and expose them to the scrutiny and use of the scientific community.

Conclusions: Drawing as pragmatist epistemology

In this chapter, I have framed drawing as a *pragmatist visual epistemology*: a mode of *inquiry*, performed with pencil or pen on paper, in which one formulates visual hypotheses and experiments with the consequences of adopting certain ideas or conceptions, or with the consequences of seeing phenomena in a certain way. In my discussion, I have explicitly built on Peirce's formulation of pragmatism and on his theory of perception, but I have also shown that these very philosophical insights were developed by Peirce *through drawing*, which offered a distinctively pragmatist counterpart to his philosophical arguments.

In the second part of the chapter, I have proposed three possible ways in which drawing can function as a pragmatist mode of inquiry in its own right: *delineating, reconfiguring* and *structuring*. Building on Lucy Lyons's practice across art and pathology, I have presented delineating as the materialization on the page of a series of visual hypotheses about observed objects or phenomena, which are iteratively corrected as the drawing unfolds on paper. Anderson-Tempini, Dupré and Wakefield's collaborative work mapping the dynamic nature of cell division has been my springboard to investigate reconfiguring as the practice of 'drawing doubt into inquiry'. Lastly, I have presented Jane Richardson's protein drawings as a case of structuring: the concrete and material practice of selectively presenting aspectual features for the purpose of comparison and classification.

Delineating, *reconfiguring* and *structuring* by no means exhaust the ways in which drawing can function as a form of inquiry in its own right. The pragmatist framework in which I inscribed them will hopefully offer artists and scientists a way of conceptualizing their own practices, and expand the list of goal-oriented activities I began sketching in this chapter with further 'visual modes' of inquiry in which drawing takes centre stage. At the same time, it is my hope that this chapter has also convinced philosophers of science to rediscover and engage with this ubiquitous scientific and artistic practice – and perhaps, following Peirce, begin to incorporate more drawing into philosophizing too.

ACKNOWLEDGEMENTS

Just like the entirety of this volume, this chapter was written during the COVID-19 pandemic. I am grateful to Gemma Anderson-Tempini, John Dupré and James Wakefield for using this remarkable book project as a way of bringing a lively interdisciplinary community together at a challenging time, for nurturing our collective enthusiasm for drawing and for their helpful comments on early drafts of this chapter. My students on the module HPSC0059 – Science Art and Philosophy asked lots of questions and offered precious initial criticism – and I can now reveal that I used them as my deadline to get the thinking on this project going! A version of this chapter was also presented at the Seminar Series of the Department of History and Philosophy of Science at the University of Cambridge. I am deeply grateful to the seminar participants for their enthusiastic reception of this work and for their constructive comments. Grant Fisher followed the vicissitudes of this chapter from Korea and helped with my initially clumsy understanding of Richardson's drawings. Of course, any errors or omissions throughout the chapter remain entirely my own responsibility. Gemma Anderson-Tempini and Lucy Lyons were most generous in

allowing me to reproduce and engage with their artworks; it was a genuine privilege to be able study their works so closely. Staff at the Houghton Library, the Ernst Mayr Library of the Museum of Comparative Zoology and the UCL Special Collections provided invaluable support with the reproductions of the archival materials. Niall Le Mage read every iteration of the various drafts for this chapter, using them as a justification to fill our flat with pages and pages of his own compulsive doodles (which – worryingly – look remarkably like Peirce's serpentine lines …).

NOTES

1. Two possible exceptions are Vorms (2011) and Fisher (2017), who show how representational formats and designs (which clearly include drawings) can serve as constraints on representational content, and matter for the kinds of inferences that can be drawn about a representational target. Historians of science, on the other hand, have been far more proactive in tackling various aspects of drawing as part of the visual cultures of science and the visual arguments put forward by scientists. The historical literature is vast, and growing, but (a selection of) classics in the field include Rudwick (1976), Kaiser (2005), Daston and Galison (2007) and more recently Nasim (2013) and Eddy (2022).
2. On the relationship between Peirce and Whitehead, particularly their respective concepts of creativity and novelty, see Brioschi (2020).
3. I follow the convention of citing Peirce's unpublished manuscripts by manuscript number and (where available) page number, as assigned in Robin (1967).
4. It was Michel Leja (2000) who first brought Peirce's doodles to the attention of Peirce scholars. The most comprehensive anthology of studies of Peirce's drawings is Engel et al.'s (2012), which includes an edited excerpt of Leja's original paper. At the same time, a whole new line of historical analysis is emerging around Peirce's drawing practices, and their sources in nineteenth-century science, art and broader culture: see for example Mirseyedi (2017) on the relations between Peirce's (1878) dot diagram (to which I return below) and the then emergent technique of the photographic halftone, Elmer (2019) on Peirce's re-mediation of Edgar Allan Poe's 'The Raven' in the manuscript 'Art Chirography' (R1539), O'Donnell (2021) on the relationship between Peirce and the Hudson River School Painter Albert Bierstadt, and Viola (forthcoming) on Peirce's diagram of 'IT' (R921) and its connections with American morphology and natural history (especially via Peirce's teacher, Louis Agassiz).
5. Peirce's logical diagrams, his 'Existential Graphs', have received far more specialized and systematic attention than his informal drawings. For a critical overview of the literature, and a contextualization of Peirce's diagrammatic practice within nineteenth-century debates on the status of diagrammatic representations, see my Ambrosio (2020).
6. For a reconstruction of the vicissitudes of the 'Illustrations', and the subsequent (unsuccessful) attempts to republish the articles in a revised form that would account for how Peirce amended his version of Pragmatism, see De Waal (2014).

7. It was famously William James who would publicly elevate Peirce's definition to a maxim of pragmatism, in an address to the Philosophical Union of the University of California in 1898. James's lecture is reprinted in Talisse and Aikin (2011), pp. 66–78.
8. Here 'EP' is the conventional abbreviation (followed by volume and page number) for *The Essential Peirce*, edited by the Peirce Edition Project, in bibliography as Peirce (1992–98). For a detailed philosophical analysis of the pragmatic maxim, see Hookway (2012).
9. Some scholars differentiate 'inquiry pragmatism' (as formulated in Peirce's 'Fixation of Belief') from 'meaning pragmatism' (as formulated in 'How to make our ideas clear'). See for example, Talisse and Aikin (2005). For an account of how the two strands of Peirce's pragmatism come together, see Dea (2015).
10. Here 'HP' is the conventional abbreviation, followed by volume and page number, to the collection *Historical Perspectives on Peirce's Logic of Science: a History of Science*, in bibliography as Eisele (ed.) (1985).
11. For an overview – and a compelling rebuttal – of critiques of Peirce's concept of iconicity in the twentieth-century philosophy, see Dipert (1996). I respond to – and try to dispel – concerns about iconicity as 'mere' resemblance in my Ambrosio (2014) and demonstrate how Peirce's account of iconic representations can contribute to broader contemporary debates on representation in philosophy of science.
12. The editors of the *Essential Peirce* have located an anonymous review of one of Benjamin Peirce's lectures, which explicitly refers to his use of this drawing:

    > The learned lecturer next showed, tracing a continuous line in such a way as to look anything but linear, but exactly similar to a batch of loaves of bread or a heap or stones, how apt we are to be deceived by our months and years and centuries about the idea of continuity, properly considered. This illustration was very obvious and striking, and drew down the acknowledgment of the audience. The error in human thought here arises from the prevalence of the law of discontinuity over continuity.
    >
    > (Anon. 1857, cited in EP2, 531, note 6)

13. Here and after, 'CP' is the conventional abbreviation (followed by volume and paragraph number) for *The Collected Papers of Charles Sanders Peirce*, edited by Charles Hartshorne, Arthur Burks and Paul Weiss, in bibliography as Peirce (1931–38/1958).
14. Indeed, Peirce himself, in response to the version of Pragmatism popularized by James, shifted the focus of his own variety of pragmatism from 'action' per se to the purposes and aims of cognition and action. See for example the 1905 essay 'What Pragmatism is', in EP2, pp. 331–45.
15. Lyons's work had an impact also on historians of medicine, to the point that 'delineation' has been used as conceptual category in the study of particular applications of drawing in surgery. See for example Alberti (2018).

16. The contrast with automated imaging will return below, in the cases of *reconfiguring and structuring*. The relationship between drawing and various forms of mechanical reproduction has been, of course, extensively studied in the literature. See for example Daston and Galison (2007), Anderson-Tempini (2014) and Alberti (2018), who builds explicitly on Lyons's delineations to provide a conciliatory view of drawing and photography in the context of surgery during the First World War.
17. The idea of re-configuring here is partly inspired by Mary Morgan's (2017) use of 'configuring' as a key characteristic of scientific narratives. And indeed, traditional diagrams of mitosis can work as established 'narratives' in Morgan's sense. Here I am interested in what happens when scientists want to explore what would happen if they disturbed or challenged a received narrative.
18. For examples of early drawings by the participants in the drawing labs, see Figure 2 in Anderson-Tempini et al. (2019), https://iiif.elifesciences.org/lax/46962%2Felife-46962-fig2-v1.tif/full/1500,/0/default.jpg. Accessed 30 March 2022.
19. Available also at https://iiif.elifesciences.org/lax/46962%2Felife-46962-fig3-v1.tif/full/1500,/0/default.jpg. Accessed 30 March 2022.
20. Available also at https://iiif.elifesciences.org/lax/46962%2Felife-46962-fig4-v1.tif/full/1500,/0/default.jpg. Accessed 30 March 2022.
21. Available also at https://iiif.elifesciences.org/lax/46962%2Felife-46962-fig5-v1.tif/full/1500,/0/default.jpg. Accessed 30 March 2022.
22. For the broader context on how a focus on taxonomy and comparison and the quest for the 'exemplary' went hand in hand specifically in protein research see also De Chadarevian and Strasser 2011. On the history and politics of molecular biology more broadly, see De Chadarevian (2002).
23. On the vicissitudes of atomic models, particularly John Kendrew's famous myoglobin model, see De Chadarevian (2018).

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3

Drawing to Extend Waddington's Epigenetic Landscape

Gemma Anderson-Tempini, Berta Verd and Johannes Jaeger

Introduction

We describe a collaboration between an artist (Gemma), a mathematician (Berta) and a biologist (Johannes), which examines the potential of drawing for understanding biological process and activates drawing as an epistemic tool to generate new images to think with (Waddington 1977; Wittmann 2011). As a case study, we consider C. H. Waddington's powerful visual representation of the 'epigenetic landscape', whose purpose it is to unify research in genetics, embryology and evolutionary biology. We explore the strengths but also the limitations of Waddington's landscape and attempt to transcend the latter through a collaborative series of exploratory images. Through careful description of this drawing process, we touch on the epistemological consequences it had on all participants, artist and scientist alike.

> When artists have tried to learn direct lessons from science, copying the visual phenomena turned up by scientific research or technically based industry, not much of value or profundity has been produced. The notions which have been more fructifying are those which have been absorbed by empathy, through the pores, as it were. And they have been expressed again by the artists not so much in any explicit exposition or diagramming of scientific ideas, but rather by living a life of implicit incorporation into a work of art – an artifact – from which the spectator again absorbs them by in-feeling more than by analysis. It is at the deep levels of the human psyche, where these kinds of communications operate, that there is the closest unity between science and art.
>
> (Waddington 1968: 72)

In the very first volume of *Leonardo*, published in 1968, Waddington tells us that

> science is something more than a collection of conceptual or practical results. It is also an activity; and its practice involves, as a very important part, the exercise of the faculties of insightful perception of natural phenomena and of the imaginative creation of new concepts.
>
> (Waddington 1968: 74)

In fact, both scientists and artists have to be able to handle concepts before they are fully and explicitly formulated, a kind of pre-linguistic exploration of ideas.

Here, we build on previous epistemological inquiries of Gemma (Anderson-Tempini 2014, 2017; Anderson-Tempini et al. 2015) as we develop and demonstrate the use of drawing in representing biological process. Our approach is informed by Gemma's experience of morphological and topological drawing, combined with Berta's training in dynamical systems theory and evolutionary developmental biology, and Johannes's process-based approach to the study of living systems. We integrate methods by artists such as Paul Klee, who have pioneered techniques for the representation of dynamics (Spiller and Norden 1973).

Alongside the practical development of drawing methods to this end, we aim to generate and stimulate discussion about the epistemological value of drawing, thus sustaining and re-vitalizing the practice of hand-drawing in contemporary scientific practice. The gradual, iterative process described in this chapter resembles the experimental collaboration that unfolds in the later chapters of this book, especially 'Drawing as intuitive mode for representing protein dynamics'. The interactions and limitations of the maze as a landscape for thinking through protein dynamics resonate with the experimental torus, knot and klein bottle landscapes drawn here.

Our different but complementary perspectives brought us to reconsider and extend one of the most powerful visual representations of biological process: Conrad Hal Waddington's 'epigenetic landscape' (Figure 3.1) (Waddington 1939, 1940, 1957). Beyond visualizing the paths taken by organisms during their embryonic development, this iconic image has the ambition to reunify embryology with genetics and evolution by showing how complex genetic and environmental changes affect the topography of the developmental landscape. Here, we tell the story of creating an extended version of this representation (Goldberg et al. 2007; Sareen and Svendsen 2010; Noble 2015).[1] In contrast to these efforts, we focus on representing complex developmental dynamics in a more accurate and realistic way through a series of six collaborative images, which identify and address challenges for visualizing the complex, multi-dimensional dynamics of evolving biological systems.

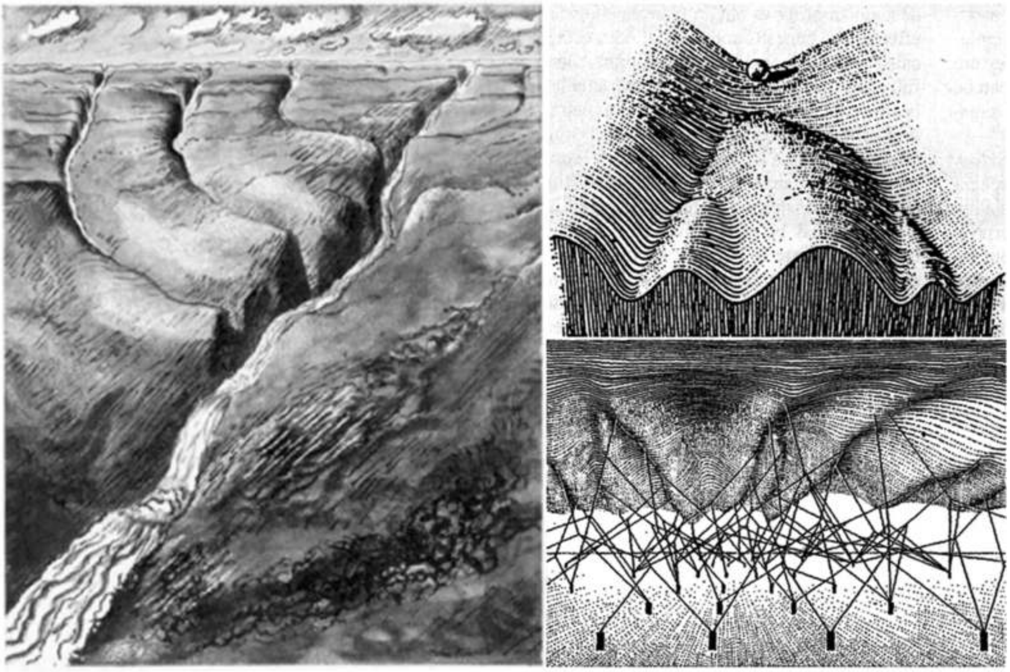

FIGURE 3.1: Waddington's epigenetic landscape. Left: drawing by John Piper for Waddington's *Organisers and Genes* (1940, Cambridge: Cambridge University Press). The original caption reads: 'Looking down the valley towards the sea. As the river flows away into the mountains it passes a hanging valley, and then two branch valleys, on its left bank. In the distances the sides of the valleys are steeper and more canyon-like'. Right: Waddington's classical depictions of his landscape from *The Strategy of the Genes* (1957, London: Allen & Unwin). Top right: Birds eye view of the landscape where the path followed by the ball represents a developmental trajectory (or chreode). The valleys represent different alternative paths to depict different developmental potentials, for example, differentiation leading to various cell types. Bottom right: by depicting the underside of the surface, Waddington illustrated the idea that genes can change the landscape during evolution. The pegs at the bottom represent genes acting on the landscape by tugging on the intertwined web of guy ropes thereby changing the topography of the valleys and ridges above. Images courtesy: tandfonline.com.

Waddington's landscape: Influence and limitations

Waddington's visualization works as follows: there is a ball on an abstract surface. This ball represents the current state of a developing biological process. It rolls downhill along valleys – called chreodes – that determine the possible trajectories the process can take. There are branching points in these valleys, one for each developmental decision, for example, whether to become a neuron or a skin cell. Each valley is bounded by steep slopes, keeping the ball on track as it is subjected to perturbations that push it away from its default path. This represents the robust or, as Waddington calls it, canalised nature of development (Waddington 1942). The landscape is not fixed: if we peek underneath the surface, we see pegs that connect to it by a network of guy ropes, which pull and alter the topography in complex, non-intuitive ways. The pegs represent genes, and the webbed ropes their influence on the developmental system. In this way, Waddington graphically combines developmental dynamics, the ball rolling down the landscape, and evolutionary dynamics, the landscape shifting underneath the ball.

While the extent of Waddington's conceptual impact on developmental and evolutionary biology is debated, his pictorial legacy is wide-ranging and profound (Baedke 2013; Fusco et al. 2014; Hall 1992; Gilbert 1991, 2000; Slack 2002; Peterson 2011). His landscape is used to integrate and structure thinking across disciplinary boundaries. René Thom put Waddington's visual intuitions on a firm mathematical basis (Thom 1976). More recently, landscape images have become widespread in stem cell biology, where they connect experimental molecular biology with systems-level models (Fagan 2012). In general, Waddington's landscape is used by researchers that apply dynamical systems theory to the study of developmental or other regulatory processes and their evolution (Huang 2012; Verd et al. 2014; Jaeger and Monk 2014). In all these cases, the landscape brings into visual focus the particular dynamic nature of biological processes and facilitates the transdisciplinary communication required to study these dynamics in an integrative and systematic way.

These examples highlight that Waddington's landscape was successful in a role that would have pleased its originator: it stimulates visual thought, enabling us to contemplate biological processes in new ways which are not yet explicitly conceptualized. To paraphrase Waddington: his artful representation helps to 'loosen the joints of the scientist's imagination', creating a space for the associative play required to introduce new concepts in theory formation (Waddington 1968).

Despite its success, Waddington's landscape suffers from several important limitations. First of all, it may be too abstract to be helpful, visually informative or imaginatively stimulating, and it is certainly difficult to connect to the experimental study of specific morphogenetic processes.[2] For example, it is not clear how the position of the ball within the landscape – representing the state of the developing system – connects to morphological changes or other indicators of system state that can be observed and measured in the laboratory. Moreover, the particular topography Waddington uses in his illustrations is intuitive, but does not hold up under mathematical scrutiny.[3]

Finally, and most importantly in our context, Waddington's landscape cannot visualize a key property of biological systems: his two-dimensional representation of the topographical surface does not accommodate complex behaviour, such as oscillatory dynamics. In the landscape, the ball always has to run downhill, while in oscillatory dynamics, the system revisits the same state or topographical location periodically. Oscillations are at the core of many fundamental cellular and developmental processes (Goodwin 1963; Goldbeter 1996; Winfree 2001; Aulehla and Pourquié 2010; Isomura and Kageyama 2014). One important example of oscillatory patterning is somitogenesis, the process by which vertebrate animals form their body segments (called somites) – adding them one by one as they grow longer during embryogenesis (Oates et al. 2012). We use this developmental process as biological anchor and motivation for our own creative process.

Extending Waddington's landscape through collaborative image-making

We explore the limits of Waddington's landscape and extend it to accommodate oscillatory and other complex dynamics, through a process of collaborative image-making that involves artist and scientist in equally crucial roles. Here, we reflect on the dynamics of this collaboration. We connect back to the epistemological nature of drawing, emphasizing its role in transdisciplinary communication and the formulation of new concepts. Finally, we discuss how our collaborative process informs both artistic and scientific methodology for the study and understanding of biological process.

We develop our collaboration through a series of six images – each a unique process of creating and exchanging knowledge through drawing. Iterative in nature, each image builds on critical discussions of the previous one.

The process began in September 2016, when Gemma was visiting the Konrad Lorenz Institute for Evolution and Cognition Research (KLI) in Klosterneuburg near Vienna. She had been invited by Johannes, who had discovered Gemma's depiction of morphological transformation in her 'Isomorphogenesis' project during a process philosophy workshop. Isomorphogenesis is an exercise in theoretical morphology consisting of a series of drawings that represent an analogue simulation of the dynamic possibilities of form (Figure 3.2). It integrates D'Arcy Thompson's grid transformations, Klee's colour gradation method and William Latham's 'Form-Synth' system for the generation of form (Anderson-Tempini 2017; Klee 1970; Latham 2014).[4] What is missing from the Isomorphogenesis series is a Waddington-style landscape that shapes and constrains the morphological transitions taking place. This observation provides a natural starting point for our exploration.

The ball in Waddington's landscape (Figure 3.1) remains the same over time as it rolls down the valleys. It does not undergo any morphological transformations. We imagined overcoming this limitation by replacing the ball moving through the landscape with an Isomorphogenesis transformation. The resulting experimental image by Gemma is shown in Figure 3.3. It reduces the level of abstraction of Waddington's representation by explicitly showing the trajectory

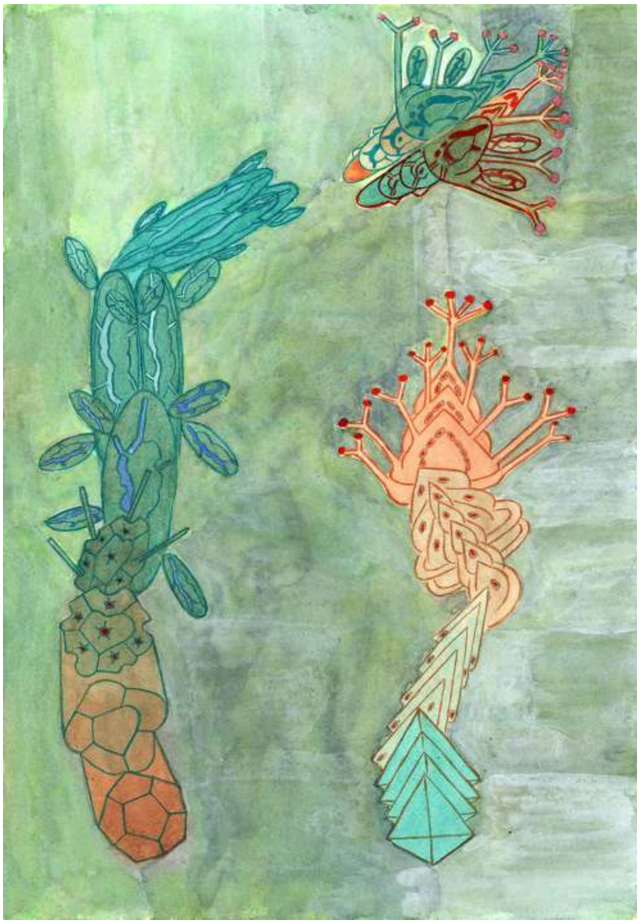

FIGURE 3.2: Gemma Anderson-Tempini, ‘Isomorphogenesis No. 2’. Watercolour on paper, 2014. Image from the Isomorphogenesis series. © Gemma Anderson-Tempini.

of morphological change (the chreode) through the valleys of the landscape. Vice versa, it provides context for the developmental processes in the Isomorphogenesis series through its explicit depiction of the landscape. However, it remains unsatisfactory, since it is still limited to a two-dimensional landscape surface, which restricts its ability to portray complex developmental processes more realistically.

Taking inspiration from their mutual interest in topology, Gemma and Berta decided to experiment with different geometrical structures as landscapes on which to draw developmental processes. The idea is that topologically complex landscapes would allow us to depict an expanded range of developmental dynamics. In particular, we wanted to find a landscape topology enabling us to represent the oscillatory dynamics involved in somitogenesis (Figure 3.4). The addition of somites to the growing vertebrate body involves repeating waves of genes being

FIGURE 3.3: Gemma Anderson-Tempini, 'Isomorphogenesis embedded in Waddington's Epigenetic Landscape'. Watercolour on paper, 2016. © Gemma Anderson-Tempini.

activated and repressed, creating oscillatory patterns of gene product synthesis, and hence dynamic travelling waves of cell state changes moving through the tissue (Oates et al. 2012). How can such periodic oscillations be represented? A torus is the natural surface topology for this purpose (Figure 3.5).

In this image, called 'Somitogenesis/Oscillations: Torus', the developmental trajectory wraps around the torus like a string. The chreode is now free to oscillate. Its cyclic colour gradation represents the oscillating levels of gene products involved in somitogenesis. A new somite is formed after each one of these cycles, elongating the embryonic axis one segment at a time. We have mentioned above that chreodes are canalized, that is, buffered against perturbations, which Waddington summarizes under the concept of 'developmental noise'. Gemma integrates a visual interpretation of such noise using artistic methods such as watercolour speckling, splashes and gestures in the image.

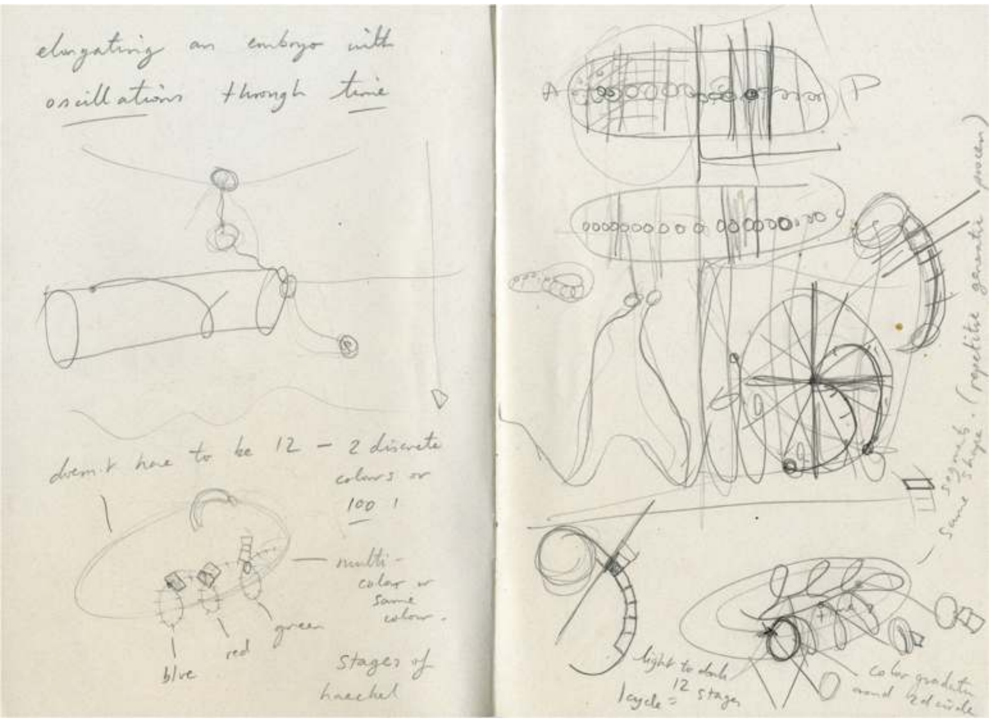

FIGURE 3.4: Collaborative drawings: Gemma Anderson-Tempini and Berta Verd, ‘Somitogeneis/Oscillations’. Pencil on paper, 2016. © Gemma Anderson-Tempini.

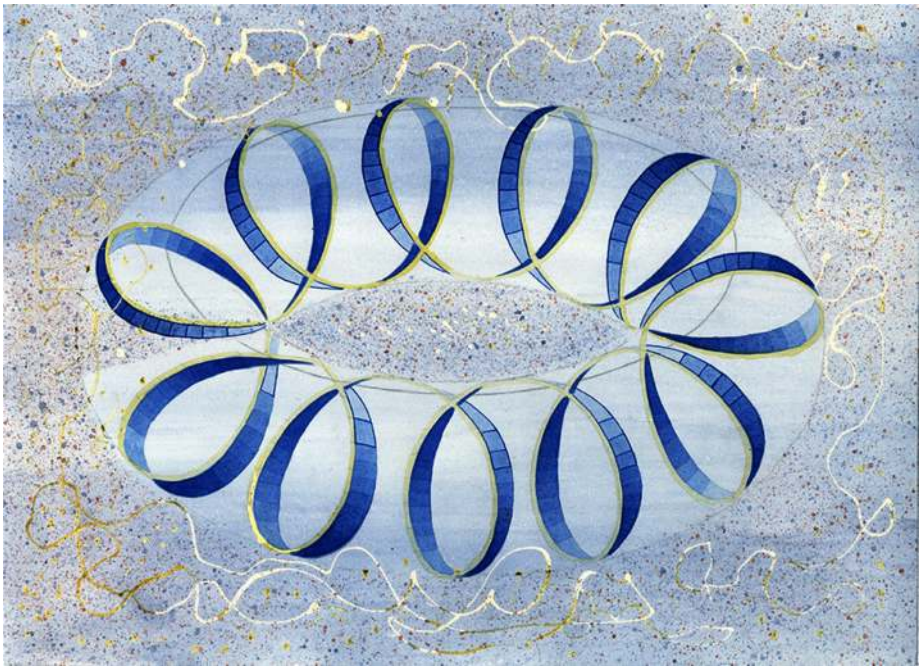

FIGURE 3.5: Gemma Anderson-Tempini, ‘Somitogeneis/Oscillations: Torus’. Watercolour and pencil on paper, 2016. © Gemma Anderson-Tempini.

The torus topology turned out to be extremely useful as a visual tool for thought. It successfully marries mathematical intuition and observation (landscape and oscillations), by releasing the landscape from the constraint of being depicted as a strictly two-dimensional surface. It allows us to experiment with various parameters like the frequency and period of the oscillations, or the diameter and length of the torus, which creates intuitions for comparing the formation of somites in different organisms, from snakes to mice. In this sense, the image constitutes a powerful new visualization tool to think about the evolution of vertebrate somitogenesis.

Although satisfied with the advances provided by the image 'Somitogenesis/Oscillations: Torus', we were still acutely aware of its limitations, as it prioritizes gene expression patterns over an accurate representation of morphological transformations. In April 2017, Gemma returned to the KLI in the context of a residency provided by KulturKontakt Austria. In the meantime, Gemma had developed a more systematic approach to creating and depicting developmental noise. Her drawing system 'Noise/Form/Gradation' provides the formal components for creating image texture with relationships analogous to biological complexity (Anderson-Tempini 2017).[5] Examples of this technique are shown in the images that follow. In addition, we wanted to experiment with even more complex topologies that would allow Gemma to introduce a more accurate representation of morphogenesis into her drawings. As a first step in this direction, we attempted to symbolize the complex, convoluted nature of organismic development by introducing knots into the torus (Figure 3.6).

Knots deliver an increase in complexity, a more comprehensive exploration of the image space on the page and an expansion of the surface area that can be occupied by the chreode. Different loops within the knotted structure could be thought of as representing different stages in a life cycle (embryo, larva, adult), each of which is subjected to variable levels and kinds of noise as indicated by the background. A complex knotted topology can also convey the sense of multiple oscillations happening at once, for instance, cell divisions and oscillatory waves of gene expression in the case of somitogenesis. Such combinations are extremely common in developmental biology. In all these ways, knotted loops provide an aesthetically pleasing compromise between complexity and simplicity. And yet, this representation still does not convey developmental trajectories in a truly realistic manner, as it does not incorporate branching or interacting paths. For this reason, Gemma decided to experiment with a network of spiralling tubes as a next step (Figure 3.7).

'Somitogeneis/Oscillations: Pathways' shows a tangled web of helical trajectories, coming in and out of focus. It highlights features of development complementary to those represented in the previous images. Figures 3.5 and 3.6 convey the cyclic and periodic nature of biological processes. The trajectories shown in Figure 3.7 may form loops as well, but only outside the focal plane of the image. Instead, different processes (marked through distinct colour gradation) connect

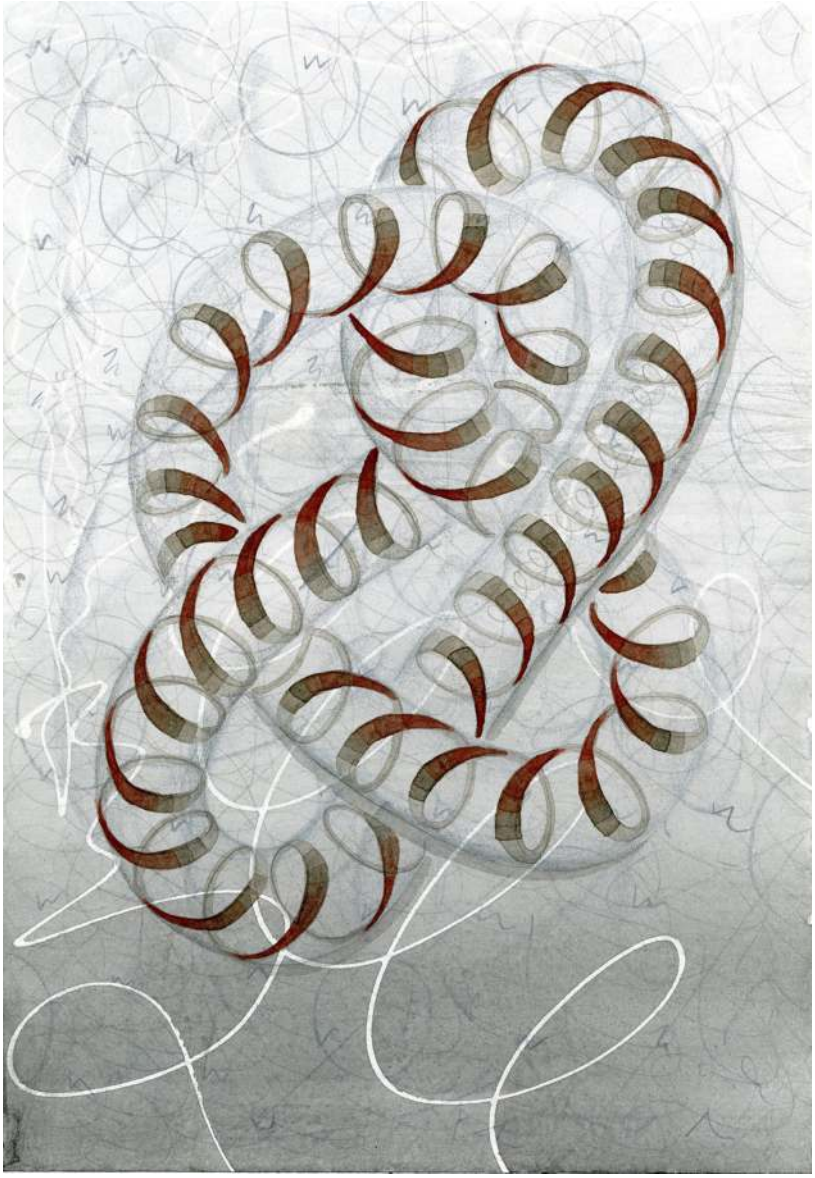

FIGURE 3.6: Gemma Anderson-Tempini, ‘Somitogeneis/Oscillations: Knot’. Watercolour on paper, 2017. © Gemma Anderson-Tempini.

and influence each other’s direction and morphogenetic transformations (drawn as simplified Isomorphogenesis-like series in some of the grey-shaded tubes). This represents induction, an important and fundamental type of developmental event, in which one tissue signals to another to alter its fate. Waddington called inductive signalling ‘evocation’ of a competent tissue (Gilbert 2016; Waddington 1940). An example of this type of interaction is the induction of lens formation by the optic cup during the development of the vertebrate eye (Cvekl et al. 2014).

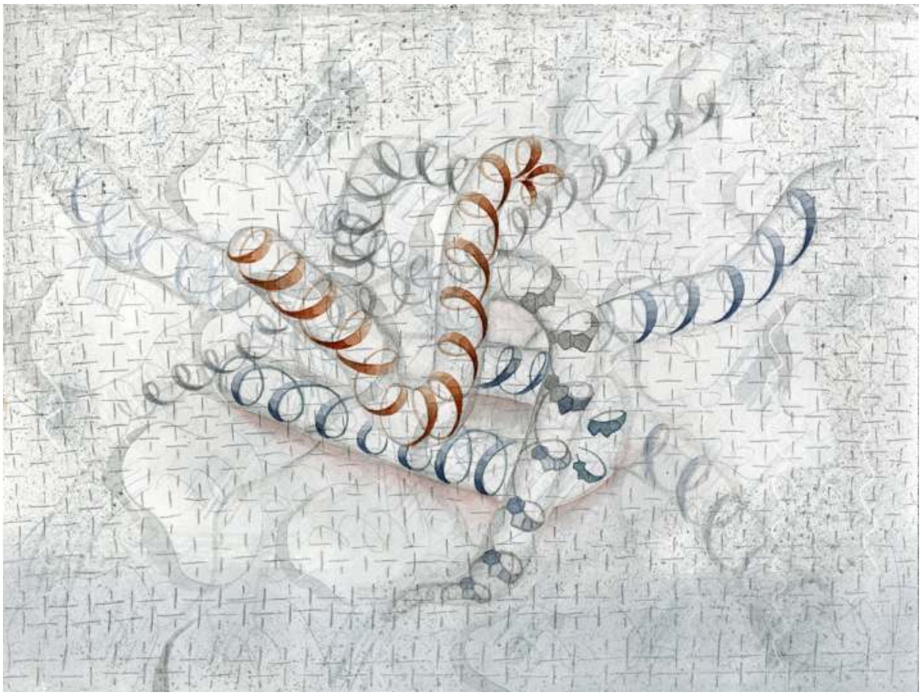

FIGURE 3.7: Gemma Anderson-Tempini, ‘Somitogeneis/Oscillations: Pathways’. Watercolour on paper, 2017. © Gemma Anderson-Tempini.

A satisfactory synthesis of Figures 3.5, 3.6 and 3.7 requires a landscape topology combining cyclic aspects with different intertwined processes. Berta suggested a topological structure that includes both: the Klein Bottle (Wolfram 2017). Like its better-known cousin, the Möbius Strip, a Klein Bottle is a two-dimensional surface that has one side only. We can understand the Klein Bottle as having a main body, which narrows to form a ‘handle’. The handle forms a cylindrical tube that intersects with the side of the main body looping back to connect the inside surface of the bottle to its outside at the bottle's base. This topology makes it possible for handle and main body to represent interactions of different processes within an intertwined cyclical trajectory (Figure 3.8).

The Klein Bottle provides a combination of torus and Waddington landscape, accommodating both oscillatory and branching dynamics. Handle and body of the bottle can be interpreted as different stages of development with fundamentally different levels of noise and canalization. The handle resembles one of the tubes in Figures 3.5–3.7. It contains a spiralling undifferentiated path, corresponding to early stages of embryogenesis. In contrast, the surface of the main body provides space for branching Isomorphogenesis transformations to unfold across an underlying Waddington landscape with valleys and peaks. This landscape is drawn on the ‘outside’ surface of the body of the bottle. The looping topology of the Klein bottle makes it possible to represent many iterations of these processes, a representation of the life cycle of an organism.

FIGURE 3.8: Gemma Anderson-Tempini, 'Klein Bottle Landscape'. Watercolour and coloured pencil on paper, 2017. © Gemma Anderson-Tempini.

There are vastly different levels of developmental noise on different sides of the bottle. The representation of canalization and noise is much more sophisticated in this image compared to Figures 3.5–3.7. Not only extrinsic noise levels vary but also the nature of intrinsic canalizing constraints. The narrow cylinder of the handle prevents branching morphogenesis, but allows for variation in the period or amplitude of the oscillation. It is difficult to predict where exactly a specific cell will exit the handle. This represents the stochastic behaviour of undifferentiated stem cells (Moris et al. 2016). On the main body of the bottle, branching morphogenesis does occur but is tightly canalized by the topography of the landscape on its outer surface. It represents the more diversified but also more canalized, late development of distinct differentiating cell populations.

In summary, the Klein bottle allows us to represent a complex knotted cyclical path with a representation of branching morphological transformations.

From an artistic point of view, it enables Gemma to extend her Isomorphogenesis method onto a landscape in combination with a depiction of stochastic oscillatory dynamics in the handle of the bottle. Seen in this light, Figure 3.8 provides a powerful synthesis of our explorations into a realistic, yet still intuitive, pictorial representation of developmental dynamics through our collaborative image-making process. In addition, it demonstrates the power of using complex topologies to represent high-dimensional developmental dynamics and the use of colour, shade and texture to represent energy fluctuations. This resonates with the development of processual images of cell division and protein dynamics in the later chapters 'Drawing the Dynamic Nature of Cell Division' and 'Drawing as Intuitive Mode for Representing Protein Dynamics'.

Conclusions

Our collaborative approach to extend Waddington's Landscape through drawing is an on-going iterative and creative process that lives in the space between art and science. The upshot of this process is not the illustration of a scientific concept, but to gain novel insights into the nature of life's processes. This does not happen through explicitly formulated conceptual analysis, as is usual within the framework of the scientific method, but rather through absorption of our images 'by in-feeling' as Waddington fittingly puts it in the opening quote to this chapter. It is a two-way exchange to which artist and scientist contribute equally. On the one hand, drawing is used as an epistemological tool and point of convergence that enables both artist and scientist to jointly develop their knowledge of the world. It provides images to think with. Complex landscape topologies, such as tori and Klein Bottles, enable Berta and Johannes to develop new intuitions and concepts regarding the transformation of morphogenesis during evolution. This is achieved through new techniques for the visualization of dynamic processes, but also the contemplative, interactive and iterative process of drawing itself. Drawing allows us to selectively highlight and explore salient features of a phenomenon. It is also a powerful constructive method for sharing insights across disciplines. On the other hand, our project reveals how the artist can make use of scientific concepts and processes – such as complex landscape topologies to represent oscillatory dynamics – to develop new approaches and methods for the visualization of dynamic form.

Modern neuroscience confirms the age-old intuition that creativity – the formation of new associations and concepts – requires playful abandoning of preconceived notions. To be creative, we must let our minds wander (Mooneyham and Schooler 2013; Kandel 2012). Sadly, our rush for productivity and the loss of space and time for contemplative practices, especially the decline of drawing in scientific practice, make it increasingly hard to achieve this sort of creative work. This hampers the creative potential of modern scientific inquiry. Our collaborative image-making process is an effort to re-establish focused creative contemplation in scientific practice. Hand drawing must not be allowed to disappear. We say this not because of its use in scientific illustration, but because of its potential as an epistemological tool to form insight and understanding, to share this understanding and to enhance creativity among artists and scientists alike.

ACKNOWLEDGEMENTS

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NOTES

1. In contrast to these efforts, we focus on representing complex developmental dynamics in a more accurate and realistic way.
2. The abstract nature of the landscape is highlighted by Slack (2002) who calls it a 'colourful metaphor' with, as Gilbert (1991) points out, 'no grounding in physical reality' (Baedke 2013; Fusco et al. 2014; Hall 1992; Gilbert 1991; Gilbert 2000; Slack 2002; Peterson 2011).
3. See, for example, J. E. Ferrell, 'Bistability, bifurcations, and Waddington's epigenetic landscape', *Current Biology* 22, R458–66 (2012).
4. For D'Arcy Thompson's theory of transformations, see chapter IX of D'Arcy Wentworth Thompson, *On Growth and Form* (abridged Canto Edition) (Cambridge: Cambridge University Press, 1992). Klee's colour gradations are described in P. Klee, *Notebooks Volume 2: The Nature of Nature* (ed. J. Spiller and trans. H. Norden), New York: Wittenborn, 1970. Latham's 'FormSynth' system for the generation of form is described in W. Latham, 'Mutator 1+2: Evolutionary art by William Latham', http://www.phoenixbrighton.org/archive/2013-2/william-latham-mutator-1-2 (2014). Accessed September 2015.
5. Noise/Form/Gradation is a systematic approach developed by Anderson-Tempini which is used to simulate artistic compositions that are analogous to developmental themes.

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4

Drawing the Origami Embryo as a Stratified Space–Time Worm

Gemma Anderson-Tempini and Alessio Corti

Introduction

In an attempt to insert ourselves into the rich history of drawing the development of embryos, we – artist and mathematician – describe our work on a more recent model, the Origami Embryo, first developed by biologist Kathryn Tosney in 1981 (Tosney 1981). Inspired by this model, we have developed a novel way to draw the embryo, by identifying topological changes and drawing these as 'slices' in a connected pictorial series that is based on topological, rather than morphological, change. We use a technical mathematical method called Morse theory to create a connected and continuous image of the process of embryogenesis, whereby embryogenesis is represented more processually as a 'space–time worm'.[1] We describe the process we followed using technical mathematical terms, which are explained in the Glossary for the reader. As our drawings are analogue and made without the aid of instruments or computers, we practice observation from 'mental images', rather than standard optical observation or observation augmented by a microscope. The process of drawing and the pictorial series prompted us to reflect on time, directionality, patterns and topology. We identify these topics as intellectual interests that artists and scientists share. Through this fundamental experimentation in art/science, we hope to promote (embodied) understanding, to continue and also transform the tradition of drawing embryos. We begin the chapter with some historical context on past representations of the embryo, discussing in particular Wilheim His's (1831–1904) innovation of cutting specimens into thin slices.

Historical representations of embryo development

Moment by moment, we cannot see change. This is true even in developing embryos, where change is relatively rapid. Since the 1870s, biologists have therefore made physical slices of embryo specimens and arranged these in sequence to construct developmental series. These series of slices or ‘sections’ were initially reproduced in a series of drawings to visualize the process of embryogenesis in unprecedented detail.

> Development cannot be observed but is constructed by selecting all those states and forms in the embryo that can be set in relationship to earlier and later forms by means of looking and comparing. The medium for such looking and comparison is the picture.
>
> (Wellmann 2017: 282)

In fact, as an historian of science, Janina Wellmann uncovers the pictorial series as a genre that provided access to much of what was new in the life sciences in the period from the late eighteenth to the early twentieth century. Practitioners arranged embryos or fossils according to formal resemblance and related the order to changes in the state over time (Hopwood et al. 2010). The pictorial series was the visual resource that enabled the relationship of forms – or ‘forms as relationships’ (Wellmann 2017: 283) – to be studied. Although Fabrici d’Acquapendente produced the earliest pictorial representations of human embryos in 1621, Soemmerring’s drawings from 1799 were the first to depict a connected series of developing embryos and are generally regarded as the first developmental series of human embryos (Hopwood et al. n.d.: 258).

> The series constructs change, in many respects: it constructs the change from one form to the next, and it constructs each individual form, which can be isolated as a single form only through its relationship to the sequence of other forms.
>
> (Wellmann 2017: 284)

Many figures of embryos are organized as an assemblage.[2] This makes visible the relational nature of development and the relational nature of any images attempting to show their developmental trajectories. The developmental series is underpinned by a pattern of repetition and variation: each image is almost identical to the preceding one but deviates from it in a single structural element.[3]

Slices, sections and models

A major change in histological practice, pioneered by Swiss anatomist Wilheim His (1831–1904), arrived with the introduction of the microtome for cutting specimens into thin slices or 'sections'. His used the microtome to visualize the internal development of the chick in unprecedented detail. This 'sectioning' of microscopical specimens became routine among anatomists and zoologists during the 1870s and has since become a standard method in morphological research (Hopwood 1999: 465).[4]

The microtome method made it possible to collect every section and to build three-dimensional (3D) wax models from discrete images. Anatomists used this sculptural process, which His called 'plastic reconstruction', as their main means for visualizing the complex structures of higher vertebrate embryos, and, alongside drawings, numerous waxes are found among the products of the work of leading early embryologists.[5] In short, the use of 3D wax models transformed scientific accounts of embryogenesis.

His suggested a series of 'simple experiments' to establish the plausibility of explaining embryogenesis through sculptural principles. For example, physical models could be made from everyday materials such as paper, rubber, leather and a lead plate to recapitulate the shape changes of the germ layers and organs (Hopwood 1999: 471). These experiments aimed to vividly visualize the bending and folding of embryonic tissues by reconstructing whole embryos from the sections. He encouraged viewing the development of the chick embryo sculpturally and mechanically, as well as imagining the bending and folding of embryonic tissue layers (Hopwood 1999: 470).

> [The] fold produces form along its line; every warp, swelling, bulge, or indentation, at every location and at every moment, directly changes the space-time coordinates of the entire embryo. Every form that closes off to the inside simultaneously opens a new space to the outside, so that every outside is also an inside. The distinction between formed and unformed matter is always only provisional; their relationship is reversed repeatedly in the course of embryogenesis. What is formed is destined not to persist as it is, but to dissolve, to change places, switch sides, transform its exterior into an interior, its surface into a body. Starting again and again, distinct yet entwined, differentiating and varying with each repetition, the folds [and the cutting and joining!] gradually make manifest the shape of the embryo.
>
> (Wellmann 2017: 276)

His believed that making helped a scientist to develop hypotheses and understanding. Following preliminary drawings, plastic reconstructions would allow scientists to give body to visual thinking. His argued that models embody anatomical knowledge: ‘The consequences of the principle of folding impose themselves in the course of such work with a much more irresistible force than through the mere contemplation of sections’ (His ‘*Mechanische Grundvorgange thierischer Formenbildung*’ in Wellmann 2017: 2, no. 16). Rejecting passive contemplation, he argued that those who wished to grasp anatomical structure had to actively work through a reconstruction to reproduce the relationships they wished to understand; they had to work not only with their brain and eyes but also with their hands. And he further argued that the activity of reconstruction produced not just a model but also an anatomist with an incomparable appreciation of form: ‘When working plastically it is indeed nearly impossible to close one’s eyes to the basic processes of the development of form’ (His ‘*Mechanische Grundvorgange thierischer Formenbildung*’ in Wellmann 2017: 2, no. 16).

The Origami Embryo model

Gemma Anderson-Tempini’s long-standing collaboration with mathematician Alessio Corti has influenced how Gemma imagines the ‘biological process’. Since 2011, we have worked on drawing higher dimensional forms and spaces. For example, in 2015, we have worked together to represent a ‘four-dimensional tree’, using the topological method of Morse theory (Anderson-Tempini and Corti 2015). When Gemma learned how important folding is in the developing embryo when reading *The Form of Becoming* (Wellmann 2017), she began to wonder if one could make an ‘Origami Embryo’ model. She then discovered that contemporary biologist Kathryn Tosney had developed an educational instruction sheet for an ‘Origami Embryo’. Tosney reiterates His’s belief in material reconstruction to give body to visual understanding and makes the following claim about her model that

> [The Origami Embryo] will help you understand the four-dimensional changes that characterize a developing embryo, as it transforms with complex three-dimensional changes over time, the fourth dimension. It gives instructions on how to fold your own complex embryo from colored paper.
>
> (Tosney 1981: n.pag.)

In 2008, Tosney developed the Origami Embryo as a hands-on pedagogical tool so that embryology students could work with a model in order to better understand complex shape changes in embryos.[6] Tosney describes how the idea came to her as a kind of ‘gestalt, all at once’, by combining the following three principles:

'(1) three different kinds of embryonic tissues fold to form the early embryo; (2) origami is a process of folding and (3) the early embryo has three tissue layers that textbooks have agreed to colour blue (ectoderm), pink (mesoderm) and endoderm (yellow)' (Tosney 1981: n.pag.). Tosney then developed the pedagogical tool for undergraduate students who find it difficult to think in three dimensions. Her aim was to help students understand how embryonic development takes place in three dimensions, as tissues interact and change properties. For Tosney, the folding action 'does not only reveal form or physical relationships, [it] actually replicates and portrays developmental processes' (Tosney 2018: n.pag.). When Tosney demonstrates the folding, she talks about the developmental interactions and processes that take place in an embryo. Further, as students fold their own embryos (and invariably make some errors), they discuss how failures in some processes will have consequences, i.e. produce particular birth defects.[7]

> As the students fold the neural tube (the process of *neurulation* also called *neural tube formation*), and tape it together at the 'dorsal' surface (the process of *neural tube fusion*), they are reproducing actual embryonic processes. In doing so they understand the need for forces to cause flat sheet of cells to change into a tube. They see (and usually inadvertently create) birth defects like 'spina bifida', a failure of the neural folds to fuse at the dorsal surface as they form the spinal cord, leaving a hole, which is a birth defect with life-long consequences.
>
> (Tosney, e-mail, 2018)

In the quote, Tosney restates His's belief in the epistemic benefits of modelling for gaining embodied knowledge or, as Myers (2015) puts it, 'kinaesthetic and affective' insight into the process of embryogenesis.[8] The process of folding also takes us back to one of Aristotle's central questions concerning embryological development, that is, 'does the embryo contain all its parts in little from the beginning, unfolding like a Japanese paper flower in water (preformation), or is there a true formation of new structures as it develops (epigenesis)?' (Peck 1943: 1949).[9]

Folding allows Tosney to reflect on specific steps in a biological process. For instance, she reflects on the consequences of the notochord (a skeletal rod supporting the body) emerging first at the anterior of the embryo:

> At these early stages, embryonic development proceeds from anterior to posterior. Because the anterior tissue interacted with the notochord (the inducer) earlier, the anterior tissues are developmentally 'older' than the posterior – they have received the signal to change earlier. As a consequence, the neural folds rise and form the neural tube in anterior to posterior order – the tube can be complete in the anterior

> while the folds are still folding into the posterior. The lateral mesoderm on each side of the embryo will form somites that emerge in anterior-to posterior order.
>
> (Tosney, e-mail, 2018)

The folding of the paper tissues around the embryo helps students to understand how the extra-embryonic membranes form to encapsulate and protect the embryo.

Tosney's Origami Embryo models the early stages (after cleavage and blastulation) of gastrulation, neurulation, formation of mesodermal primordia, formation of the amnion and the chorion, formation of the gut and yolk stalk, formation of the allantois and formation of the lateral body walls. It does not include the later stages of embryogenesis, for two reasons: First, the early stages establish all of the major tissue precursors; thereafter, few of the organs change their form by folding. Second, there are relatively few embryonic 'inductions' in later development that can be represented with simple folding of flat surfaces.

The Origami Embryo model contributes to a long history of using paper, wax and plasticine in teaching embryology.[10] Tosney did not try to use plasticine for modelling, because, as she contends, this would not have enabled the students to model change in form over time. For Tosney, the manipulation of paper mimics actual embryonic processes, as changes to the paper form echo the processes of embryonic folding and metamorphosis.

Taking the Origami Embryo into topological drawing

Fascinated by Tosney's Origami Embryo, Anderson-Tempini brought the following question to Corti: 'Can we draw the origami embryo in 4D using Morse theory?' And so we progressed from the Origami Embryo model to topological drawings. In this section, we provide an account of our decisions and actions while working together on this question during a studio residency in Ireland in 2017.

Our starting point was Tosney's Origami Embryo and her instructions for recapitulating the early stages of the development of a chick embryo through a sequence of folding, cutting and joining (stapling) operations with sheets of paper. As we followed Tosney's instructions and made the origami, we realized that the exercise is analogous to constructing a mathematical 'shape' – in mathematical language, a 'topological space' – through a sequence of 'surgery' operations known as 'cutting' and 'pasting' in mathematical language.[11]

We made the paper model until we understood the instructions, and then we made our own drawings (of the changing topology of the embryo) of Tosney's model.

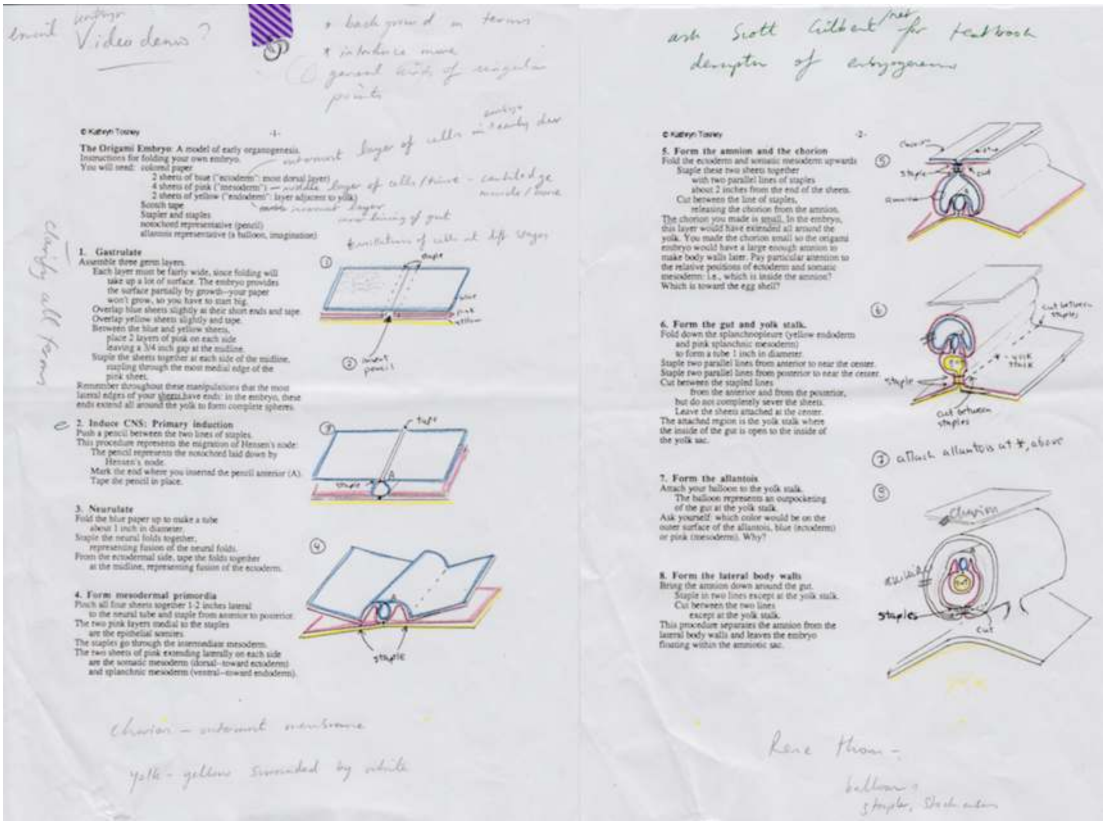

FIGURE 4.1: Kathryn Tosney, ‘Origami Embryo’ (1981) with colour and notes by Gemma Anderson-Tempini. A4.

FIGURE 4.2: Gemma Anderson-Tempini and Alessio Corti, ‘Paper models of Origami Embryo’ (2017).

Our drawings follow Tosney’s colour coding: blue, pink and yellow correspond to ectoderm, mesoderm and endoderm, respectively.[12] Moreover, our own drawings simplify Tosney’s model by only representing a 2D cross-section of the

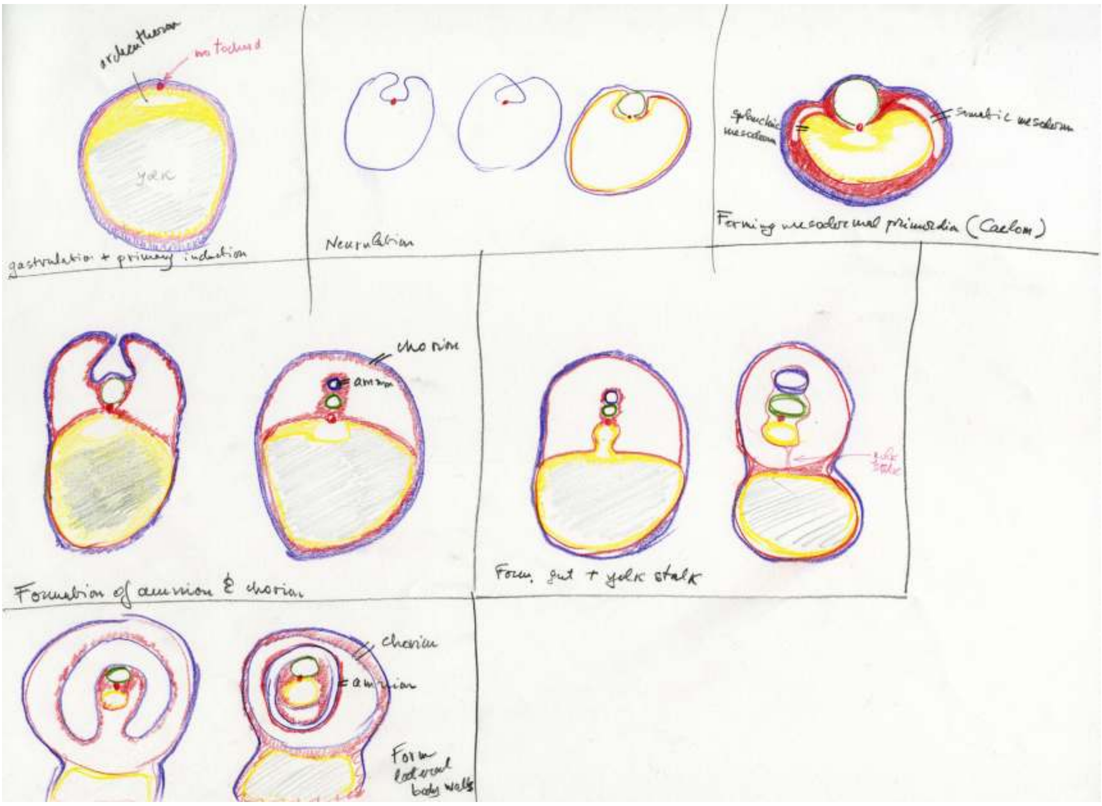

FIGURE 4.3A: Alessio Corti and Gemma Anderson-Tempini, ‘Drawings of the changing topology of the embryo corresponding to Tosney’s model’. Pencil and colour pencil on paper, 2017.

developing Origami Embryo. Hence, they lose some information – but not too much. As we will see below, only two developmental steps remain unobservable to us, the formation of the yolk stalk and of the allantois (as seen in the beautiful drawings of Karl Ernst von Baer, Figure 4.4). On the other hand, we were able to draw the entire sheets of cells that extend around the yolk. This allowed us to model the whole of the embryo, which Tosney’s origami did not: ‘remember throughout these manipulations that the most lateral edges of your sheets have ends: in the embryo, these ends extend all around the yolk to make complete spheres’ (Tosney 1981).

Most importantly for us, by plotting the time direction as if it were a third spatial dimension, we were able to re-assemble the drawings of 2D sections at different times into a 3D image of a ‘space–time worm’.[13] This 3D shape offers us a connected and continuous image of the process of embryogenesis. The image of the ‘space–time worm’ allows us to visualize in one whole a 2D process that happens in time; the 2D cross-sections – snapshots of the embryo at different moments – as a timeless 3D worm. Rucker has discussed this method of visualization at

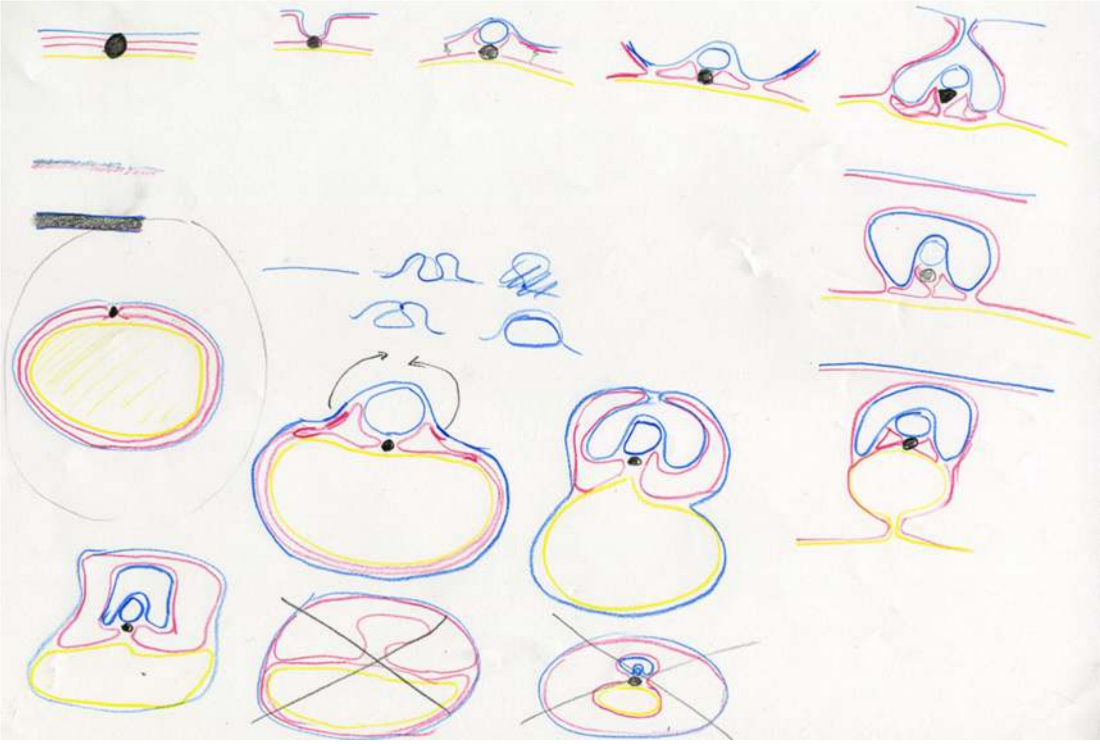

FIGURE 4.3B: Alessio Corti and Gemma Anderson-Tempini, ‘Drawings of the changing topology of the embryo corresponding to Tosney’s model’. Pencil and colour pencil on paper, 2017.

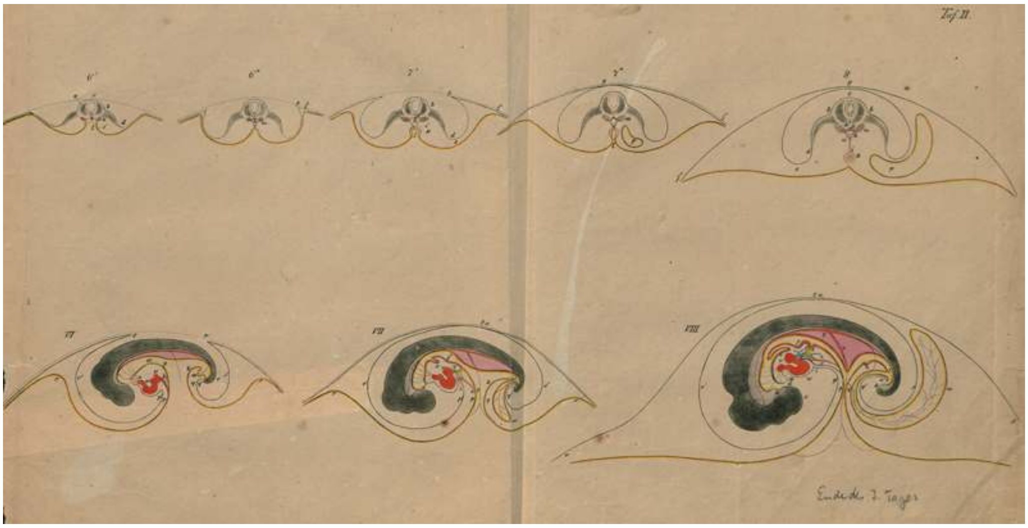

FIGURE 4.4: Karl Ernst von Baer and Heinz Christian Pander, ‘Detailed drawing of chicken embryonic development’, 1828.

some length in ‘Time as a Higher Dimension’ (Rucker 1977: 57–66). By the same logic, an n-dimensional (unspecified number of dimensions) process that happens through time can be ‘visualized’ as a timeless (n+1)-dimensional worm.[14,15]

As we have already noted, the process of joining and cutting sheets of paper is literally and immediately interpretable as the construction of a space through a sequence of cutting and pasting (also called ‘attaching’) operations – sometimes called surgeries by mathematicians – like in standard topology (see Glossary). More precisely still, that these operations take place in a prescribed time sequence suggests that the operations occur at the critical values of a function like in Morse theory – a mathematical theory that studies an (n+1)-dimensional shape by considering the n-dimensional level sets of a function on it. A typical example when the shape in question is the 2D surface of a landscape ($n = 1$), the function is the altitude function, and the 1D level sets are the contour lines that represent points at the same altitude.

Of special importance in Morse theory are the critical level sets. To continue the example of a landscape, these are the contour lines that contain a peak, a trough or a saddle point. The level sets immediately before and after a critical level set are topologically distinct, and one is obtained from the other by a surgery operation. In the case of the embryo, $n = 2$, the shape is the 3D space–time worm, the function is time, and the 2D level sets are the snapshots of the embryo at given times – representing the embryo at those times. This immediately brings us back to our 4D tree project. Following this line of thinking, we have turned Tosney’s model from an ‘Origami Embryo’ to a ‘Topological Embryo’.

We think of the embryo as a stratified 3D space with a boundary (see Glossary). The interior of the space, i.e. the fluid in the embryo, which is also the largest (open) stratum, is coloured grey. The boundary surface has three connected components (see Glossary), with each a stratum coloured blue, pink and yellow according to whether it corresponds to tissue made of ectoderm, mesoderm and endoderm (with the exception that we have painted the interior of the neural tube green). The smallest stratum is 1D and it corresponds to the notochord. We have not modelled the finer structure of the interior (see comment no. iii in the limitations discussed below).

Next, we chose a typical slice through the embryo, perpendicular to its axis. This then gave a surface, i.e. a 2D space with a boundary. In other words, we chose to model the evolution not of the whole 3D embryo but of a 2D cross-section of the body of the embryo perpendicular to its axis, as anticipated above.[16]

We then depicted this model in a sequence of fourteen 2D drawings (Figure 4.5). The fourteen drawings were then re-assembled into a 3D drawing (Figure 4.6), which we call the space–time worm.

We now offer an extended technical commentary on the fourteen 2D (Figure 4.5) drawings; following this, we discuss the space–time worm, that is, the re-assembled drawings in Figure 4.6.

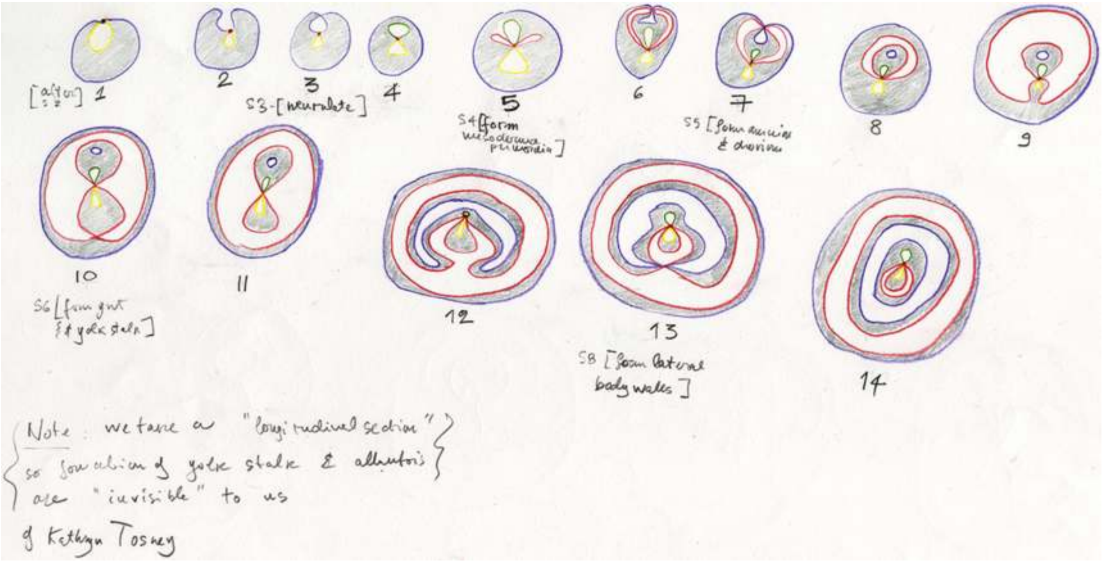

FIGURE 4.5: Alessio Corti and Gemma Anderson-Tempini, '14 drawings of the changing topology of the embryo'. Pencil and colour pencil on paper, 2017.

Each of the fourteen drawings is the level set of a (stratified) Morse function on a (stratified) 3D space. This 3D space is the space–time worm that re-assembles in one image the complete evolution in time of a 2D cross-section of the embryo. The 3D space–time worm is drawn in Figure 4.6. The Morse function is time: its value at a point of the space–time worm records the time at that point, and a level set at a given time is a picture of the 2D cross-section of the embryo at that particular time. The fourteen drawings depict a sequence of fourteen snapshots of the 3D space at fourteen separate times in sequence. The space 'content' (flesh, largest open stratum) is coloured grey while the main boundary components (skin) are coloured blue, red and yellow according to the type of tissue that they are made of.

The Morse function has five critical values that correspond to five of the values of the time at which the five developmental stages occur. The cross-section of the embryo changes topology precisely at those times. The five cross-sections at these five values of time are called critical cross-sections and depict the five critical stages in the development of the embryo.

There are three types of topological change, which in the drawings of the space–time worm (Figure 4.6) are realized by one of three operations: attaching a bridge-shaped form (Figure 4.7A [Fig. A in illustration]), attaching an inverted bridge (Figure 4.7C [Fig. B in illustration]), or attaching the object depicted in Figure 4.7C (Fig. C in illustration). The three stages are shown in Figure 4.7A, 4.7B and 4.7C (A is an inverted Y shape with thickness, B is a Y shape with thickness and C is a bucket shape.)

The five critical stages are, in turn:

1. Fusion of the neural folds (step 3 in Tosney's instructions), achieved by attaching a bridge shape.
2. Formation of mesodermal primordia (step 4 in Tosney's instructions), achieved by attaching two Y shapes in sequence.[17]
3. Separation of chorion from amnion (step 5 in Tosney's instructions), achieved by attaching a bridge and then an inverted bridge.
4. Formation of the gut (step 6 in Tosney's instructions), achieved by attaching an inverted bridge.
5. Formation of lateral body walls (step 8 in Tosney's instructions), achieved by attaching a bridge and then an inverted bridge.

Below we offer more detailed commentary on the fourteen 2D slices in Figure 4.5:

1. The image represents a slice of the embryo after gastrulation (see Glossary) and primary induction: the blue boundary component is the exterior surface of the embryo; the red dot is the notochord and the yellow boundary component encloses the archenteron.
2. This image is topologically equivalent to 1. It shows the emergence of the neural folds.
3. This is the first critical slice, picturing the embryo at the exact time when the neural folds fuse.
4. In this image, taken after the neural folds have fused, we can see the neural tube enclosed in the green boundary component.

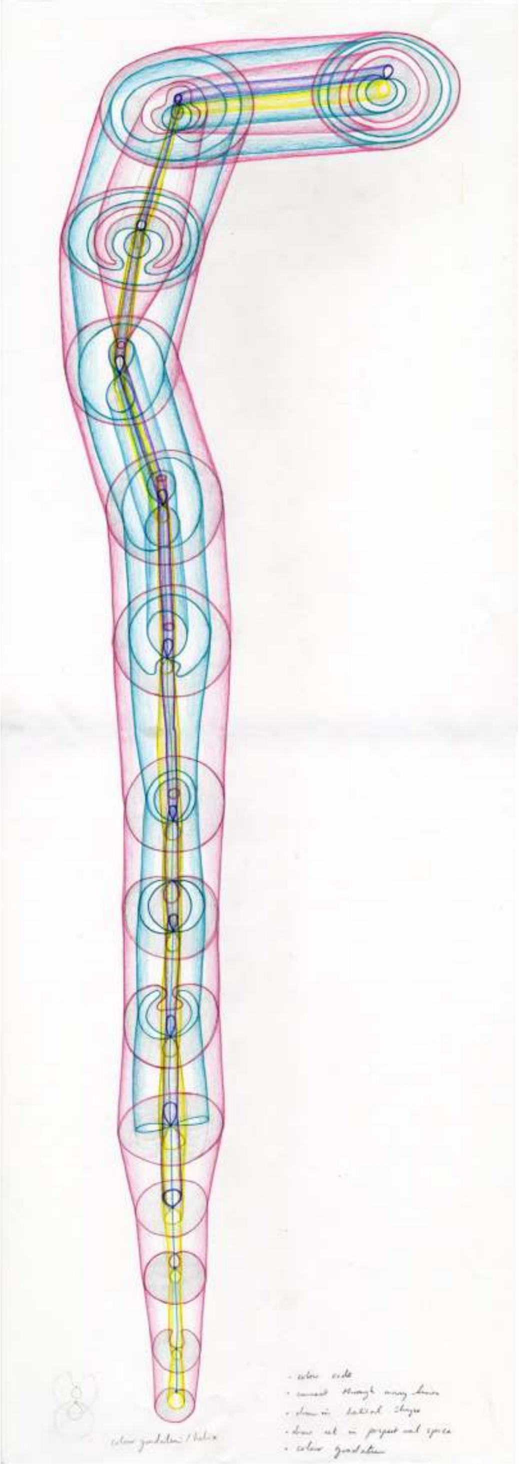

FIGURE 4.6: Gemma Anderson-Tempini, 'Embryo as a stratified space-time worm'. Colour pencil on paper, 2017.

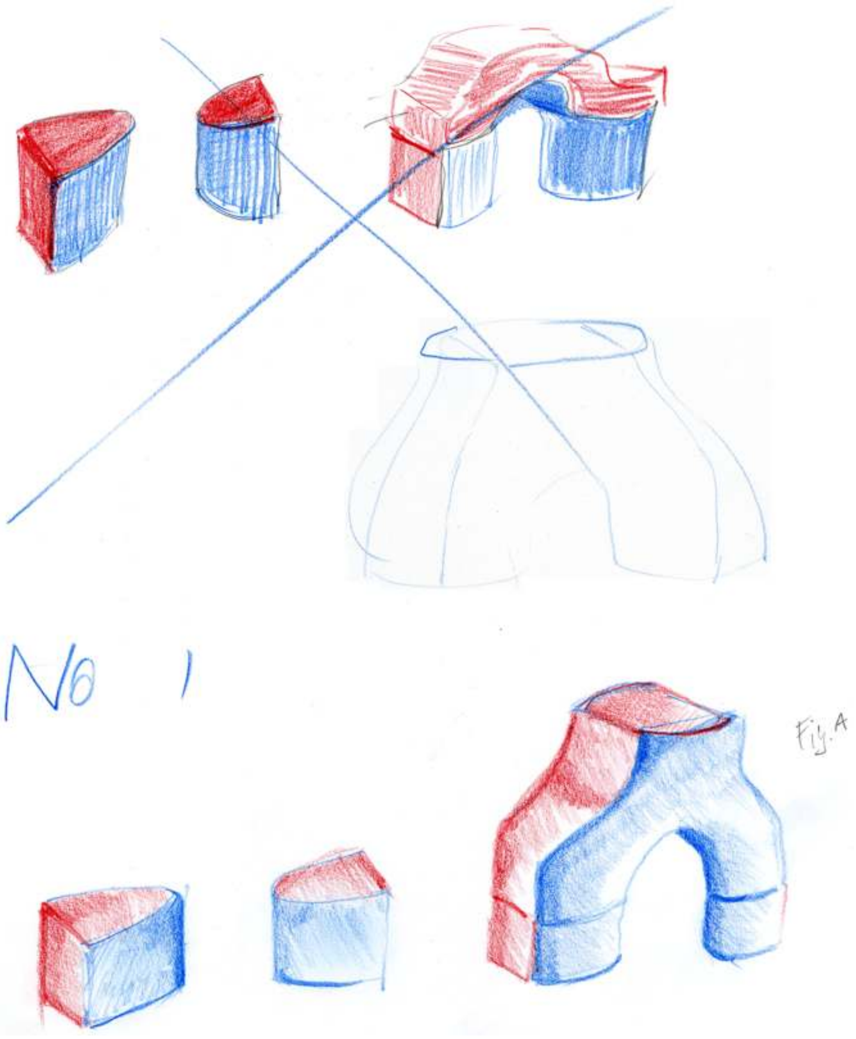

FIGURE 4.7A: Alessio Corti and Gemma Anderson-Tempini, 'Fusion of the neural folds by attaching a bridge shape'. Pencil and colour pencil on paper, 2017.

5. This image depicts the critical slice corresponding to the formation of the mesodermal primordia.
6–8. These images show the formation of chorion and amnion. Here 6 is topologically equivalent to 5; 7 is the critical cross-section.
9–11. These images show the formation of the gut, enclosed in the yellow boundary component. (Image 9 is topologically equivalent to 8 and image 10 is the critical slice.) Images 12–14 show the formation of the lateral body wall of the organism:
12. This image is topologically equivalent to 11, and it shows the time just before the wall is formed; image 13 is the critical cross-section.

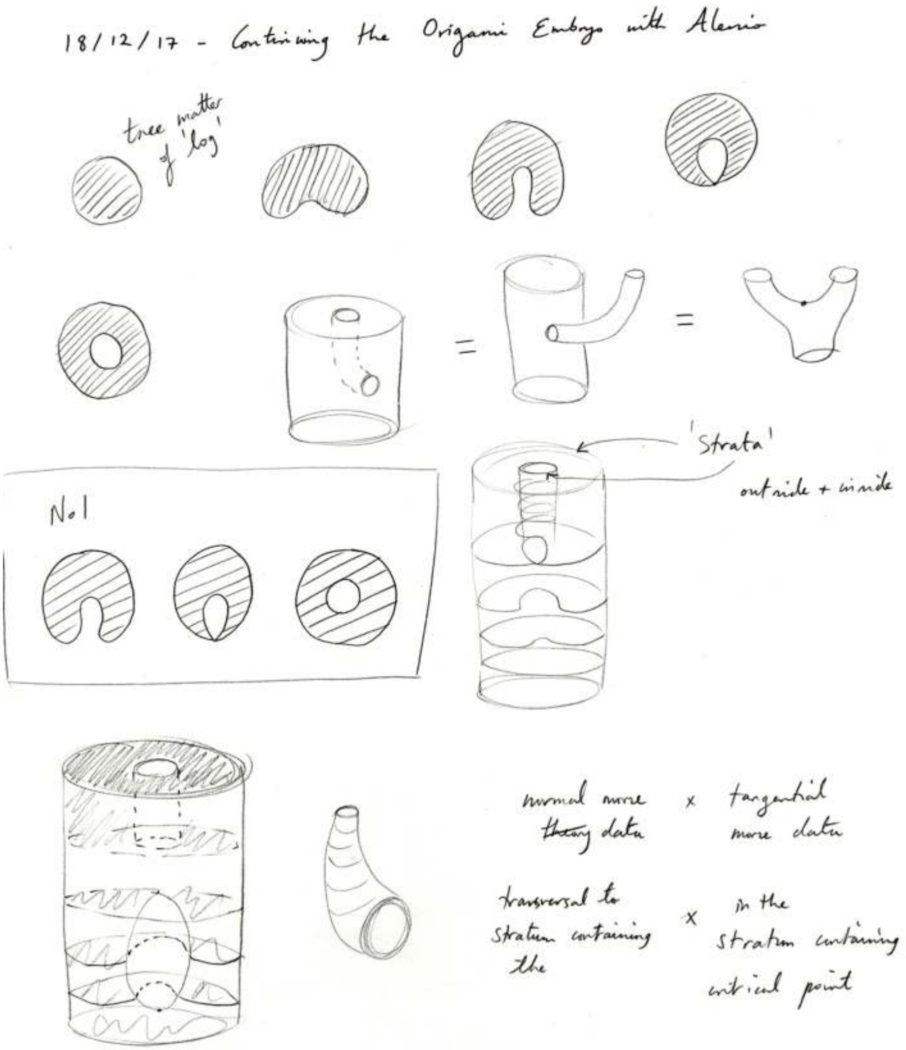

FIGURE 4.7B: Gemma Anderson-Tempini, 'Formation of mesoderma primordia by attaching two Y shapes in sequence'. Pencil on paper, 2017.

Finally, after all this drawing and having practised playing through the sequence in our own minds, we re-assembled the slices into a 3D stratified space in a similar way as we did when drawing a 3D tree in Anderson-Tempini and Corti (2015) from an 'instruction sheet'.[18] We drew the 3D space in question, which we call a 'space–time worm' (Figure 4.6).

In this final image, the process of topological change in development during the first five days is represented by a single 3D image of a 3D stratified space. This is analogous to what we did with images of 3D and 4D spaces that we called 'trees' (Anderson-Tempini and Corti 2015). The spaces in the 4D tree had no interior, i.e. they were not stratified. Following our previous collaborations, it had been our

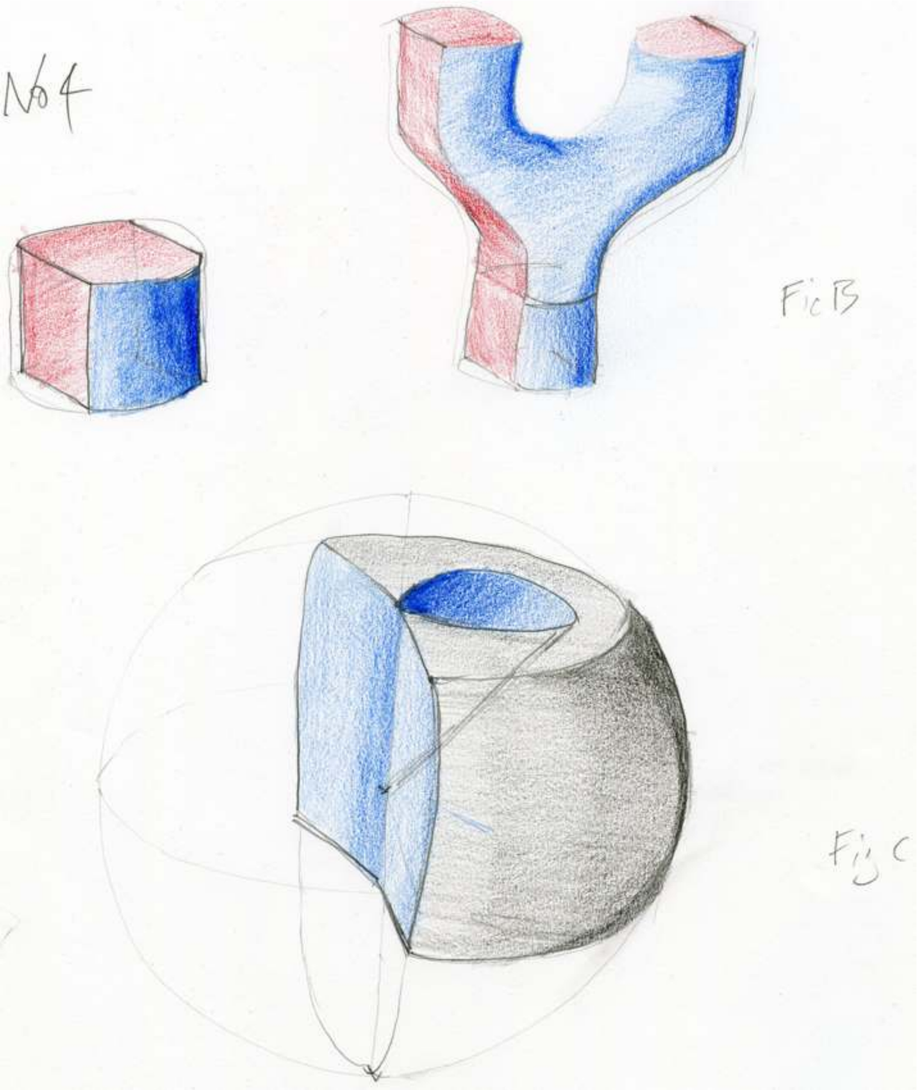

FIGURE 4.7C: Alessio Corti and Gemma Anderson-Tempini, ‘Formation of the gut by attaching an inverted bridge’. Pencil on paper, 2017.

intention from the start to make a connected image that would permit us to visualize the previously disconnected sequence of changes in topology all at once. This is completely unlike making an animated movie from a sequence of stills, because the movie still unfolds in time, whereas our image is timeless. ‘The whole is no longer subjected to time but rather possesses time within itself’ (Wellmann 2017: 83).

The image depicts a 3D space with a boundary that contains a sequence of snapshots, taken at different times, of the embryo as subspaces. One could say that the 3D space was there all along, implicitly constructed from instructions determined by the stills interpreted as level sets of a function, but through our image, we see it for the first time. Learning to visualize this three-manifold had been our goal all along.

Some limitations of our topological model are:

(i) The starting point of our model is the stage after step 2 of Tosney's instructions. We have not tried to model steps 1 (gastrulation) and 2 (primary induction) of Tosney's instructions. In our initial drawing, the singular point represents a section of the notochord. In our model, gastrulation is taken for granted: we have not attempted to be specific about the finer structure of the interior and have merely recorded the tissue type (blue/red/yellow) of the boundary surfaces (with the exception that the interior of the neural tube is painted green). The details of gastrulation happen on a microscopic scale that does not lend itself to modelling by topology. However, Gemma attempted to draw gastrulation as a follow-up project during a visit to the Leptin Lab, and lots of plasticine modelling (which does not capture topological change) focuses on gastrulation.[19,20]

(ii) Our model does not represent the formation of the yolk stalk (step 6 in Tosney's instructions) and the formation of the allantois (step 7): as already discussed, these events take place outside our chosen embryo slice and are thus unobservable as far as our model is concerned.

(iii) We have not attempted to model somite formation, nor any of the later stages of development that are documented. Like gastrulation, the creation of somites and the subsequent microscopic details of organogenesis do not naturally lend themselves to topological modelling (as somites form along the axis of the developing embryo, the process of somite differentiation is not visible in the slice we have chosen as topology ignores cells on the boundary surface, i.e. the skin). Somite formation and organogenesis take place inside the grey inner material (fluid) of the space, and we did not attempt to model these processes. Tosney's instructions likewise do not attempt to model these stages.

(iv) The final image is a 3D stratified space. More precisely, it is a singular 3D stratified space, the singular zero-stratum being located at the point that represents the notochord. The time function and the process of re-assembling the space from its time slices are an instance of stratified Morse theory (Goresky and MacPherson 1988).

Experiments in art: Drawing embryogenesis as a connected process

Up to this point, the drawing still, literally, depicted an abstract model of chick embryo development. The resulting image nonetheless provides a faithful and

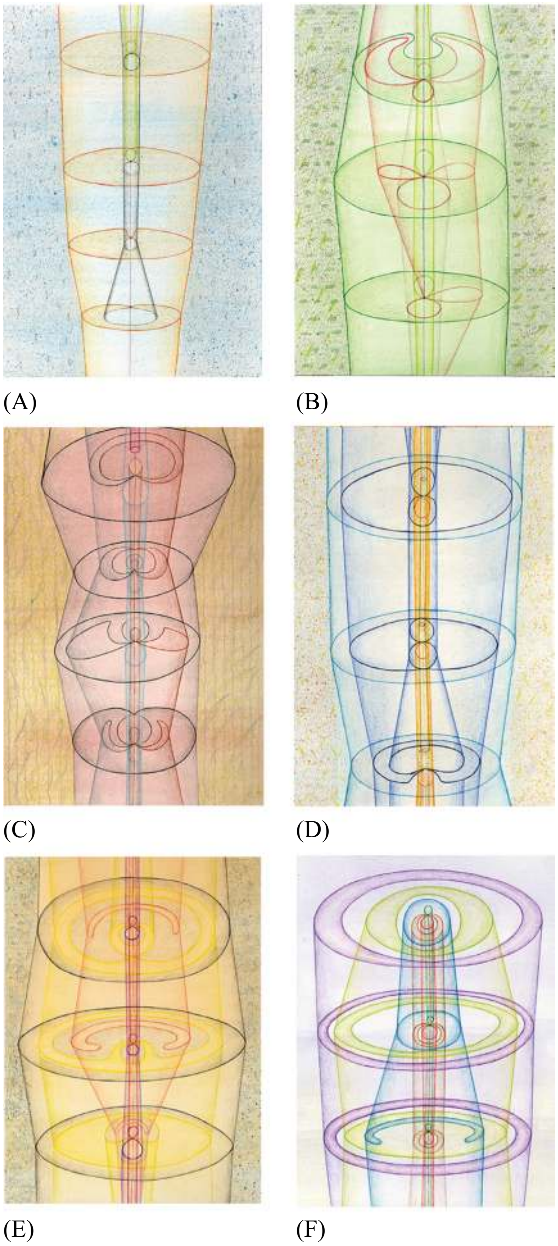

FIGURE 4.8A–F: Gemma Anderson-Tempini, 'Embryo as a stratified space-time worm'. Watercolour and colour pencil on paper, 2018.

novel visualization of a particular scientific model. From this point on, Gemma developed the image further through experiments in drawing, painting and printmaking by taking artistic freedom to improvise with the pattern and 'liberate' it from its scientific context and constraints.

What is the overall artistic impression given by our final image?

Instead of drawing transformation through a series of isolated stages, Gemma connects the positions, each drawing a succession of forms connected as a 'single fluid movement': a series and a variation on the pattern. The sense of variation arises out of the relationship *between* stages in the series. The perception of change is something relative, possible only in the alternation of image and void, pose and formation.

> One surveys so many single moments that, taken together, yield a whole picture, but these single moments are so delicate that it is difficult to put them into words, and when recounted individually, they do not create any effect, any conviction; one simply has to see the whole itself.
>
> (Dollinger n.d.: 284)

By moving through the series of images, viewers can appropriate and interpret for themselves a concept of development with the changes that are gradually coursing through the structures (Wellmann 2017: 318). Drawing helps us to think about development as a set of visual relations. The series is underpinned by the rule of repetition and variation: each image is almost identical to the preceding one but deviates

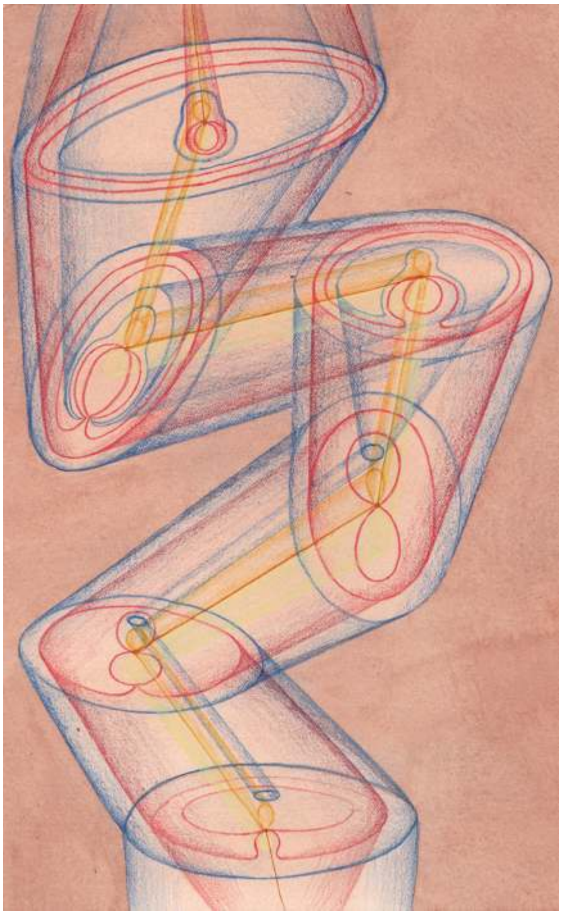

FIGURE 4.9: Gemma Anderson-Tempini, ‘Various pathways that the embryo can take in development’. Watercolour and colour pencil on paper, 2018.

in a single structural element. Wellmann argues that, in the relationship of forms within a series, the interval or gap between the pictures acquires constitutive force, and further that the connection between the shown and the not shown, ‘the bridge between fullness and emptiness’, generates change, and the spatial alternation of image and gap produces a new ordering of time. This order, the principle behind the series, Wellmann argues is its rhythm (constructed rhythm). Rhythm is regularity; the intrinsic oscillation between repetition and variation, between past and future (Wellmann 2017: 319). For Wellmann, the conception of development as rhythmical motion thus added a new dimension to the biological world. The dimension that made it possible to understand the peculiarity of organic life as something that was structurally bound, but that simultaneously brought forth its own uniqueness again and again – ‘in the hidden interstices, in the gaps of perception’ (Wellmann 2017: 324).

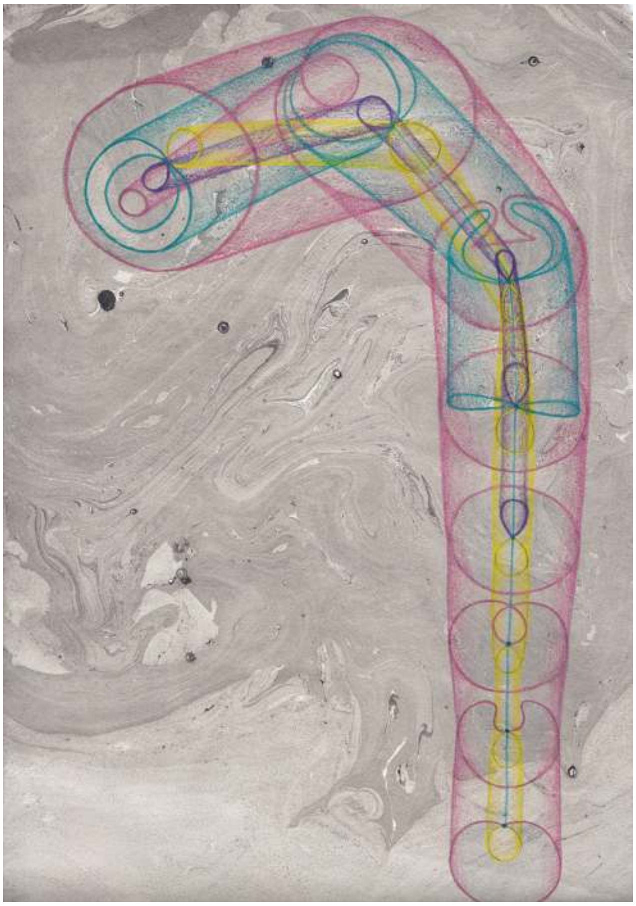

FIGURE 4.10: Gemma Anderson-Tempini, 'Embryo as a stratified space-time worm – with noise'. Colour pencil on marbling paper, 2018.

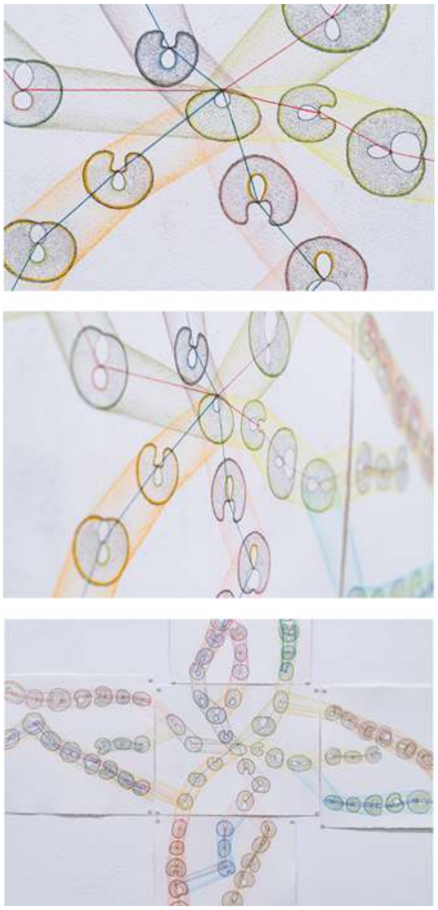

FIGURE 4.11A–C: Gemma Anderson-Tempini, 'Modular Embryo/Garden of forking paths'. Copper etching with colour pencil and watercolour, 2018.

Contrary to the common belief that moving images help us to see change, we contend that stillness that helps us to see movement and change. Change is constituted through the relationality of the picture series. The series is a synthesis and analysis of development at once. Development is both the individual form and the series of forms – it is stasis as much as flow. Locating development in the images we have created is to imagine development as a pictorial relationship. It is the relationship between the visual forms that produce both the individual stage of development and development as a whole – simultaneously and in mutual dependence (Wellmann 2017: 233). This leads Wellmann to imagine the organism as 'something that never remains identical with itself, that never stands still, that perpetually moves forward, that passes through a particular set of changes in a kind of cycle' (Wellmann 2017: 144).

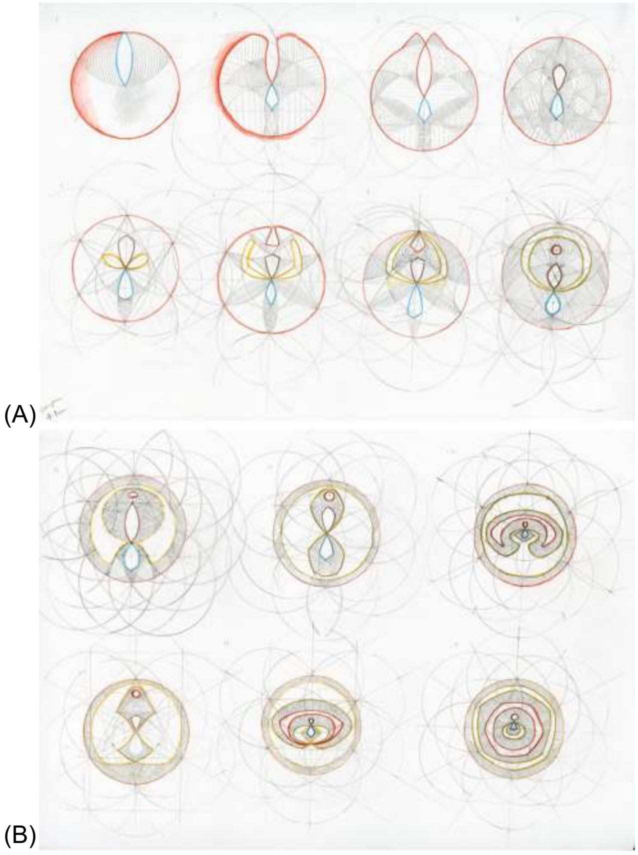

FIGURE 4.12A and B: Gemma Anderson-Tempini, ‘Embryo Compass 1’ and ‘Embryo Compass 2’. Colour pencil on paper.

This repetition of forms, with slight variation in a connected series, is comparable with the evolution of organisms and artworks. In the work of the artist Paul Klee (1879–1940), the process of formation is represented alongside the external appearance of the subject. In *Fishes* (1921), for example, the progression of form takes place within the body of the fish itself, giving expression to time, movement and growth simultaneously. Klee was attracted to the underwater world of fishes because of the freedom of movement they enjoy (in any direction, whereas humans are much more restricted). The ‘fishness’ of the fish is maintained through the transformations; each stage bears a unique gradation of colour, repetition of the same form seen from different angles and scales, moving forwards, backwards and sideways, creating a feeling of emergence from a dark background. Klee’s watercolour washes elevate the forms to a resonant poetry. The fishes appear transparent; we see the traces of their development through a clear membrane, like a cell, representing Klee’s penetration of form beyond superficial appearances. In these works, Klee allows for many perspectives: above, below and alongside the forms.

Klee's *Suspended Fruit* (1921) can similarly be read as an abstract ontogenetic series. The abstraction in this work is not from observation, but from an insight into the growth of plants from thought and experience itself. In *Fugue in Red*, the circle is analogous to the embryo that, through a series of transformations, becomes a different shape (adult). This happens through a progression of forms, grading from white to black, through pale pink, pink, deep pink, purple, grey-purple, grey and black. The transformation from triangle to square, through the repetition of forms with slight variation, becomes an analogy for evolution conceived as descent with variation, while echoes of form grade through shadows and colours in other directions and other aesthetic dimensions. Klee's expansive way led to the dimensional promotion (or inversely, de-motion) of his work from 3D–2D to 4D–2D (here the fourth dimension is time). In this interpretation of

FIGURE 4.13: Paul Klee, *Suspended Fruit*. Watercolour on paper, 1921. *In Paul Klee's Enchanted Garden* (2008), Berne, Switzerland: Klee Zentrum. Public domain.

Klee's work as an ontogenetic or developmental series, I am mapping this biological concept onto artistic practice (Anderson-Tempini 2017: 135–64).

Taking inspiration from Klee, in our embryo drawing, we see development through a pictorial relationship – including oscillations between relations. The rhythmic order of the drawing is a structure of deviating patterns. 'The essence of rhythm is the fusion of sameness and novelty; so that the whole never loses the essential unity of the pattern, while the parts exhibit the contrast arising from the novelty of their detail' (Whitehead in Wellmann 2017: 25).

Discussion of intellectual interests that artists and scientists share

Time and directionality

The final drawing we produced using this method has its own temporal order within itself and therefore defines its own specific rhythm. Time is implied through change, but change is not time – change has its own internal time (Galton 2018). At this point we wonder, what are the philosophical implications of contemplating an n-dimensional process that happens through time as a timeless (n+1)-dimensional 'worm'? This question is explored by Rucker in *Time as a Higher Dimension*:

> To get a good mental image of space-time, let us return to Flatland (Abbott 1884). Suppose that A. Square is sitting alone in a field. At noon he sees his father A. Triangle, approaching from the west. A. Triangle reaches A. Square's side at 12:05, talks to him briefly, and then slides back to where he came from. Now, if we think of time as being a direction perpendicular to space, then we can represent the Flatlanders' time as a direction perpendicular to the plane of Flatland. Assuming that 'later in time' and 'higher in the third dimension' are the same thing, we can represent a motionless Flatlander by a vertical worm or trail and a moving Flatlander by a curving worm or trail [...]. We can think of these 3D space-time worms as existing timelessly.
>
> (Rucker 1977: 58)

When looking at the embryo drawings, we pondered the following questions about time and directionality: Why have we started at the bottom of the page? And why is time assumed to have an upwards direction? Surely we could start anywhere on the page and, as time has no set direction, the image could progress in any, or in fact all, directions? Why only move in one direction? Why not many? What about a drawing that starts with one embryo slice and evolves in many directions, into many variations of the process?

‘The Garden of Forking Paths’ is a short story by Luis Borges (1998), and his ideas of ‘forking paths’, of ‘several futures’ and of a ‘labyrinth of symbols’ all align with how we imagine our embryo drawing taking many possible paths in the abstract maze-like landscape of development.[22,23]

> The garden of forking paths is an incomplete, but not false, image of the universe […] an infinite series of times, a growing, dizzying web of divergent, convergent and parallel times. That fabric of times that approach one another, fork, are snipped off, or are simply unknown for centuries, contains all possibilities.
>
> (Borges 1998: 85)

The medium of printmaking (specifically copper etching), like development, allows for repetition with variation each time and for an infinite number of combinations of elements within the image. Inspired by these ideas, Gemma created a ‘modular etching’ of parts that join together in many possible ways, thus making visible at least a portion of Borges possible ‘web of divergent, convergent and parallel times’: ‘I leave to several futures (not to all), my garden of forking paths’ (Borges 1998).

Topological problems interest artists and biologists as well as mathematicians

Surely among the most important goals of every geometrical instruction is the strengthening of the faculty for spatial imaging and the power for spatial modelling (Schoenflies 1908). Topology requires us to think about form in space. As such, it is natural to use drawing to explore topological questions and ideas. ‘Topologists sketch freely, both to develop their own intuition and to communicate that intuition to others’ (Anderson-Tempini et al. 2015: 442). Yet, topological ideas, problems and methods are rarely explored explicitly at art school (unless an art/maths course is offered, for example at Central Saint Martins).[24] We regard our drawing experiments as ‘analogue models’ of a kind that construct links between the domains of art, maths and biology/embryology. To access the rich territory of topology, we therefore recommend that the artist seek out collaborations with mathematicians.

Patterns can give a lot of freedom for creativity

In this project, we have devised a new way to draw the embryo as a pattern of connected ‘slices’. This pattern can be varied through infinite artistic experiments and variations, for example through colour, scale, shape, texture, material and medium. Anterior and posterior configurations of the body during development and developmental pathways can also be revised through further collaboration with embryologists (mutations, etc.).[25]

Drawing an embryo as a series of ‘slices’ could be considered a form of reductionism, but this was not our intent. Rather, we are confident that the pattern of ‘slices’ opens up unconventional ways of exploring the life of the embryo that lead us away from reductionist thought. When drawing a tree in the fourth spatial dimension (Anderson-Tempini and Corti 2015), we felt that we had somewhat unlocked a key to explore the nature of the tree indefinitely, and, in drawing the embryo, we experience the same feeling again. Like the 4D tree, our image of abstract embryogenesis brings to mind Goethe’s idea of the primal plant:

> The Primal Plant is going to be the strangest creature in the world, which Nature herself must envy me. With this model and the key to it, it will be possible to go on forever inventing plants and know that their existence is logical; that is to say, if they do not actually exist, they could, for they are not the shadowy phantoms of a vain imagination, but possess an inner necessity and truth. The same law will be applicable to all other living organisms.
>
> (Goethe 1970: 310)

Drawing builds a model of an ‘Ur-embryo’ without attempting to give an objective account of how embryogenesis happens but instead offering a visual model of some of the ways it could happen. In this way, art can follow the same ‘rules’ as the developing embryo; repetition with creative variation. We draw the embryo as a persisting dynamic pattern by freeing ourselves from the conceptual confines of the physical object.

The repetitive act of drawing itself allows for a meditation within the image-making process. This practice relates to Buddhist tantric image-making, for example the yantra or pala mandala as images of meditation and learning, where the image becomes a by-product of the concentration and embodied awareness of the maker. In the drawing and re-drawing of this pattern of the developing embryo, the image becomes one of meditation and learning like ‘Embryo’.[26] (Figure 4.11). The woodcut by Japanese artist Yoshida Toshi (1956) merges the neural folds and the somites from different developmental stages into one image. In his image, the ‘Embryo’ also resembles a musical instrument and functions as a more abstract image for contemplation. The repetitive act of drawing facilitates meditation on the nature of the embryo. In this way, the image seeps into waking life and a newfound ‘sense’ of the embryo is embedded as a mental image.

Recapitulation: What can mathematicians and developmental biologists learn from this work?

In this chapter, we have interpreted embryogenesis with the help of stratified Morse theory. A stratified $(n+1)$-dimensional space – i.e. the space–time worm – with stratified Morse function *is* the embryogenesis of an n-dimensional 'embryo' that, like Goethe's *Urpflanze* ('primal plant'), 'may not exist and yet could exist' (Goethe 1946: n.pag.). Our drawings represent the embryogenesis of the chick. It would be interesting to produce similar sequences for other embryos and see what is different. From here, a few perhaps impressionistic, naive questions remain that may be worth exploring for a scientist:

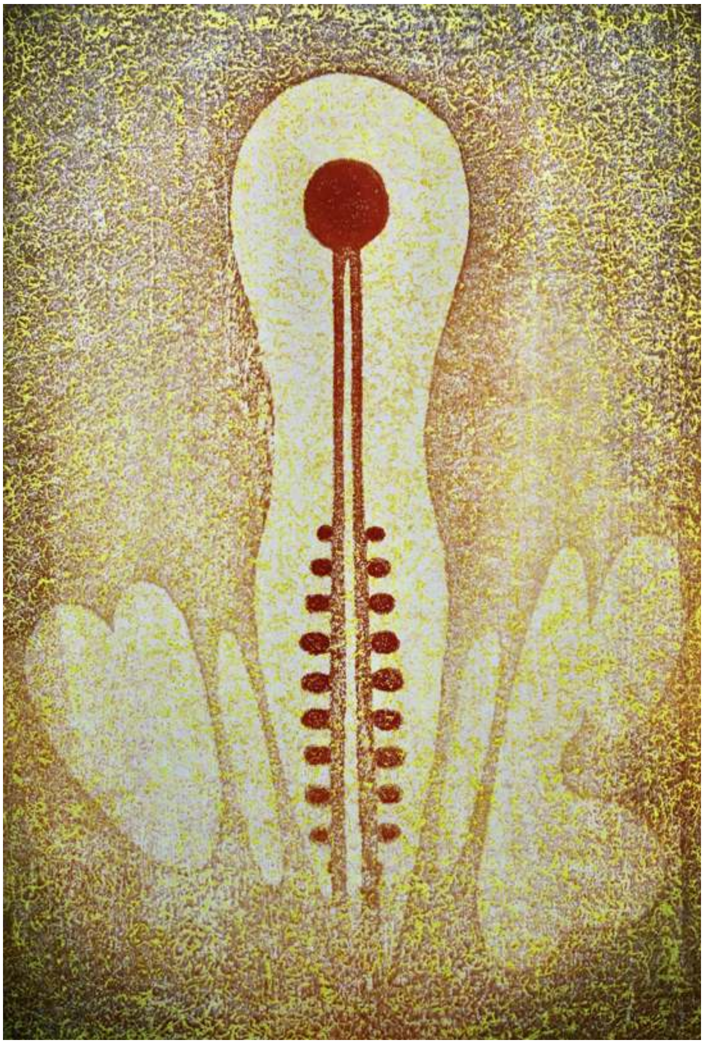

FIGURE 4.14: Yoshida Toshi, 'Embryo'. Woodcut on paper, 1956.

(a) Topological invariants of the space–time worms, such as the homology groups, are invariants of the corresponding embryogenesis process. Can these invariants be used to distinguish the embryogenesis of embryos that actually happen in nature?
(b) Even if the space–time worms are topologically equivalent, the Morse functions themselves can be topologically distinct, corresponding to processes (embryogenesis) that take different paths to produce the same fully formed organism. Are these ideas helpful for understanding what actually happens in nature?
(c) A reasonable point of view is that embryogenesis ends with the 'fully formed organism'. Can we imagine topologically distinct processes – i.e. the space–time worms are topologically distinct – that produce the same fully formed organism? Does nature in some sense optimize the process by choosing the simplest topology?
(d) Can we set up a precise mathematical version of Waddington's 'landscape', partitioned into walls and chambers (creodes/pathways)? Can we interpret a biological mutation as crossing a codimension-one wall?

On the usefulness and production of images in science

The final question we ask is, what can we learn, as scientists and as artists, from what we did, and more specifically from the final image we produced?

Many scientists (and especially biologists) find images useful in teaching, communication and, especially, as epistemic tools in scientific practice. An image is, after all, a representation, and scientific practice is largely about the creation and manipulation of representations. An epistemological benefit of our origami embryo drawing is that it allows students to trace changes in time by connecting the stages in the series. By applying mathematics to biology, we have created abstractions that allow for the comparison of forms as a 'pattern language' and therefore potentially open up new ways of making images of processes across scales. With our example of careful and thoughtful joint image creation between art and science, we hope to provoke discussion about image-making methods and the implementation of such methods in both artistic and scientific practice and education.

A short note for mathematicians

For geometers or topologists, it is natural to attempt to model embryogenesis by means of Goresky and Macpherson's stratified Morse theory (1988). The whole of embryogenesis is represented by a 4D Whitney-stratified space (with boundary) – the space–time worm – together with a Morse function on it. The

Morse function is time and the 3D slice at time *t* is a Whitney-stratified space (with boundary) representing the embryo at time *t*. Stratified Morse theory is masterfully summarized in Sections 1.1 and 1.2 of the Introduction of *Stratified Morse Theory* (Goresky and Macpherson 1988). The theory is extremely flexible and makes it possible to model each of the developmental steps as critical points occurring at critical values of the Morse function. The space–time worm is built in a sequence of operations, each corresponding to a critical value of the Morse function, consisting of attaching the Morse data of that critical point. The Introduction explains how to understand Morse data as a product of normal and tangential Morse data. In this note, we did not attempt to picture the whole 4D space, preferring instead to picture a 3D cross-section (this compromise was motivated by the ease of visualization). The 3D space is singular at the point of formation of the mesodermal primordia and, according to stratified Morse theory, we must take that point to be its own zero-stratum: Figure 4.7C (Fig. C in illustration)? is a picture of the Morse data at that point – this is the normal Morse data as there is no tangential Morse data in this case. (More precisely, we imagine the change to happen in two steps very near in time each modelled by attaching such a picture.) The attachment of bridges and bridge inversions are topology changes that take place in a non-singular stratified space, and they are therefore easier to visualize. In both cases, the Morse data (the bridge) is a 3D parallelepiped (a solid ‘brick’), topologically the product of an interval (normal Morse data) and a square (tangential Morse data).

Glossary of mathematical terms

Note: this glossary of mathematical terms does not provide the mathematical definition of the term. Instead, it gives one or more metaphors: concrete representatives of that concept that symbolize it.

Connected components: We use this terminology in the context of a stratified space with a boundary, where there are different types of boundaries: for example, in a biological organism with different types of skin; for instance, an outer one (epiderm) and an inner one (endoderm). These different types of boundaries are the connected components of the boundary stratum.

For *function; level set; critical level set; critical point; critical value; Morse function; surgery; cut; paste; stratified Morse theory; see Morse Theory*.

For *Homeomorphism* see topology.

Morse Theory: A mathematical theory that allows to study a space by considering the [level sets] of a [function] on it. A typical situation is when we visualize a landscape by a contour map. The space in question 'is' the landscape, the function is the 'altitude' of a point in the landscape and the level sets are the contour lines – representing points at the same height. The [critical level sets] are the contour lines that contain a [critical point], that is, a peak, a trough or a saddle point: the corresponding height is then called a [critical value] of the function. The level sets before and after the critical value are topologically distinct. We always assume that the function is a [Morse function], that is, every critical level contains only one critical point: for example, no two peaks have the same height, a saddle point and a peak never occur at the same height, etc. The level just above a critical value can be obtained from the level set just below by a simple topological operation called [surgery] where we [cut] a piece and [paste] a new piece. In the key example of this chapter, the space in question is the final space–time worm, the Morse function is time, the level sets are the snapshots of the embryo at a given time, etc. The version of Morse theory appropriate for stratified spaces is called [stratified Morse theory] and was developed by Goresky and Macpherson (1988).

Space: The mathematical word for shape. In this note, we speak of [stratified space with boundary]: a shape consisting of various types of 'tissue'; for instance, an 'interior' and an outer (or inner) 'skin'. The interior and the skin are then two [strata] of the space. The [boundary] consists of the strata that 'bound' the shape (e.g. from the outside, which is not actually part of the shape).
For [stratified space with boundary], [stratum], [boundary] see [space]

Topology: The mathematical study of shape, i.e. space in this note. A branch of mathematics concerned with those properties of geometric configurations (such as point sets) that are unaltered by elastic deformations (such as a stretching or a twisting) – called [homeomorphisms]. For example, a teacup is topologically equivalent to a doughnut: if the teacup were made of dough, we could elastically deform it into a doughnut – in doing this, it is crucial that we preserve the 'hole' in the handle.

Biological terms

Gastrulation: gastrulation is a phase early in the embryonic development of most animals, during which the blastula (a single-layered hollow sphere of cells) is reorganized into a multi-layered structure known as the gastrula.

Yolk: the yolk (also known as the vitellus) is the nutrient-bearing portion of the egg whose primary function is to supply food for the development of the embryo.

ACKNOWLEDGEMENTS

We thank the Cill Rialaig Project (Artist Residency Project in Kerry, Ireland) for a residency in September 2017, during which Anderson-Tempini and Corti collaborated on this project. We acknowledge the Engineering and Physical Sciences Research Council (EPSRC) funding for Corti's research, and we thank Scott Gilbert, Nick Hopwood, Janina Wellmann and Kathryn Tosney for invaluable comments.

NOTES

1. The 2D time slices combine into a 3D space–time worm: a shape that is drawn in this chapter for the first time.
2. In the sense that it takes more than one image to make development visible; however, many images of embryos, which are understood to be or to have been developing, are of single embryos.
3. Repetition followed by variation was Richard Owen's model for the production of homology, as well as the Britten-Davidson model for repetitive DNA.
4. Later a critique of sectioning came that through 'mindless' sectioning, students were losing the capacity to visualize whole organisms, and with this a loss of appreciation for how they functioned in environments (Hopwood: 476).
5. The apothecary and physician Adolf Ziegler began modelling embryos in the early 1850s as Ecker's assistant, but in 1868 left his university position to start an independent studio. Styling himself a 'plastic', or sculptural, 'publisher', he worked after professors' specimens, drawings and models, and always had these 'authors' approve 'proofs' of models that thus became indispensable to teaching and research (Buklijas and Hopwood 2018).
6. Tosney's origami model is in fact using the techniques of Kirigami, i.e. folding and cutting (in origami there is no cutting).
7. For example, when students push the pencil down the midline of the anterior to posterior axis (i.e. the developing notochord), it 'induces' the neural tube at the midline of the embryo. This models the process of 'primary induction', which induces the overlying ectoderm to create the precursor of the central nervous system, the neural plate. As a consequence of the notochord's interaction with the ectoderm that it contacted directly, that ectoderm develops new properties (it has been 'induced'). This will then thicken to become the 'neural plate' and the edges next to the ectoderm will fold up to form the 'neural folds' which will fuse at the midline and separate from the ectoderm (which heals over it).

8. For example, the folding of the paper tissues around the embryo helps students to understand how the extra-embryonic membranes form to encapsulate and protect the embryo.
9. Originally a footnote in the English translation of Aristotle's *De Generatione Animalium*.
10. For recent plasticine-based teaching in the context of the history of wax modelling: http://www.sites.hps.cam.ac.uk/visibleembryos/s3_3.html.
11. A note about the use of mathematical language in this paper: we use mathematical language as a way to systematize metaphors. So, for example, the mathematical concept of a 'level set' stands for all of the following concrete representatives: a contour line on a map; an individual image from a sequence of images constituting a CT scan; an instance of a series of snapshots of a process evolving in time. Each of these concrete representatives of the mathematical concept can serve to symbolize it. We wish to convey that by making mathematical statements about level sets, we make statements about all of these concrete representative situations. We invite the reader to meet the mathematical concept in its representative.
12. Blue ectoderm, red mesoderm and yellow endoderm are the standard that has been used in every embryology book over the past two centuries. von Baer used red mesoderm and yellow endoderm although think he had four germ layers.
13. The 2D time slices combine into a 3D space–time worm: a shape that is drawn in this chapter for the first time. In fact, this drawing is the main product of the paper.
14. $(n+1) = (n+\text{time})$.
15. If we had drawn the whole the embryo as a series of 3D rather than 2D cross-sections, then the worm would have been an image visualized in the fourth spatial dimension, which would require considerable exertion of the imagination to visualize. We see both the physical 2D slices and the 3D space–time worm as instances of a general mathematical theory – Morse theory. Seeing in this light allows one to systematize analogies between embryogenesis and other processes such as landscape formation. If the 2D slice model is a tree, then Morse theory is the conceptual apparatus that allows you to see the forest. It should be clear that this opens up possibilities such as the translation of concepts, directions of scientific inquiry, problems and methods from one discipline to another.
16. This is different to the traditional 2D slicing of an embryo as we are taking the 2D slices into a different framework, using the conceptual aid of mathematical theory to build and connect the slices in the mind rather than in physical form.
17. It would be possible to achieve this in one step by attaching a double Y shape. In any case, the critical point must be its own zero-dimensional stratum.
18. This can be imagined as an abstract spatial stacking together something like live-cell imaging.
19. See 'Imaging by computer and drawing by hand', https://thenode.biologists.com/imaging-by-computer-and-drawing-by-hand/science-art/.
20. http://www.sites.hps.cam.ac.uk/visibleembryos/s3_3.html.
21. Artwork photographed in 'GAA: Holistic science and wisdom tradition' exhibition, The Exchange, Penzance, Cornwall, February–May 2018.

22. Like the cell (ball) drawn within the valleys of Waddington's epigenetic landscape, the embryo can roll in many directions. In John Pipers image of Waddington's metaphor, we do not see the many 'possible' paths that could be taken.
23. In dynamical system theory, a phase space is a space in which all possible states of a system are represented, with each possible state corresponding to one unique point in the phase space. For mechanical systems, the phase space usually consists of all possible values of position and momentum variables. The concept of phase space was developed in the late nineteenth century by Ludwig Boltzmann, Henri Poincaré and Josiah Willard Gibbs.
24. http://maths.myblog.arts.ac.uk/.
25. For example, Tbx6-deficient mouse embryos, where three neural tubes develop and the somites develop as neural tubes.
26. An image montage of Hensen's node (a node, or primitive knot, is an enlarged group of cells located in the anterior portion of the primitive streak in a developing gastrula. The node is the site where gastrulation, the formation of the three germ layers, first begins. The node determines and patterns the anterior–posterior axis of the embryo by directing the development of the chordamesoderm).

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5

Drawing the Dynamic Nature of Cell Division

Gemma Anderson-Tempini, James Wakefield and John Dupré

Introduction

The cell is the fundamental unit of life and cell division is one of the most fundamental biological processes. For life to proliferate, the genetic material – the DNA – needs to be accurately replicated and then accurately divided into two identical complements, alongside the other contents of the cell and the cell membrane itself. Cell division encompasses the way in which the cell first aligns and then segregates its duplicated chromosomes – a process termed 'mitosis' – and then the physical constriction of the cell membrane to ultimately generate two, usually equal, daughter cells (Figure 5.1). Movement over time and the dynamic re-organization of the cell are central in all aspects of this process. Following DNA replication, the cell generates and organizes many thousands of dynamic protein filaments (microtubules) that coalesce to form a complex structure called the mitotic spindle (Duncan and Wakefield 2011). The spindle exerts physical force upon the duplicated chromosomes within the cell, aligning them to the centre of the spindle. Once all the chromosomes are 'balanced' at the centre of the spindle and correctly attached to microtubules from each half of the spindle, they are co-ordinately segregated through movement away from each other towards the poles of the spindle. This chromosome segregation is usually followed by cytokinesis, during which the cell membrane itself constricts at the equator of the cell until two new cells are generated. In this way, the duplicated chromosomes are resolved back into individual copies, and the contents of the original cell are equally apportioned between the two new daughter cells.

The archetypal visual description of mitosis was communicated by Walther Flemming in a series of elegant drawings between 1878 and 1888 (Figure 5.1A; Paweletz 2001). Recent advances in imaging have led to significant improvements in our understanding of this process (Figure 5.1B). However, despite these developments, two-dimensional (2D) representations of mitosis and cell division remain virtually unchanged (Figure 5.1C). Moreover, advances in imaging technologies have not left the role of the researcher untouched; whereas cell biologists once used drawing to synthesize what they had seen looking down the eyepiece in thousands of microscope images of cells, the advent of highly sensitive cameras built into microscopes now means that they observe post-processed images on computer screens and instead focus on measuring what the screen reports. While this technology allows for imaging of molecules and sub-cellular structures that would not otherwise be possible, it has consequences; it moves the scientist further away from the process being observed and eliminates an element of exploratory imagination that drawing once promoted. Thus, whereas the training of cell biologists was previously centred around direct observation and participation, the technological and methodological advances in live cell imaging, image acquisition and quantitative image analysis now position the scientist as an observer, topographer and measurer (Figure 5.2A–C). Though this shift may be justified in terms of the removal of subjective elements associated with

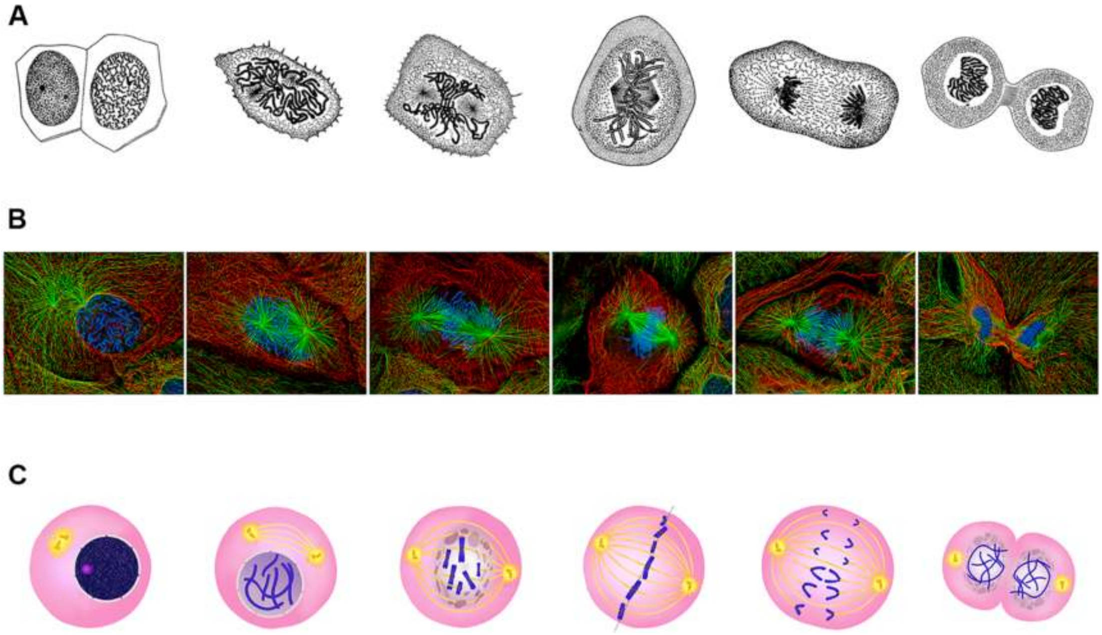


FIGURE 5.1A–C: Classical representations of cell division. (A) Walther Flemming's drawings of eukaryotic mitosis, 1888 (image adapted from Walther Flemming, CC0). (B) Confocal fluorescent microscopy images of new lung cells during mitosis in culture (image: Alexey Khodjakov, CC BY 4.0). (C) A diagram of the stages of cell division (image: Ali Zifan, CC BY-SA 4.0).

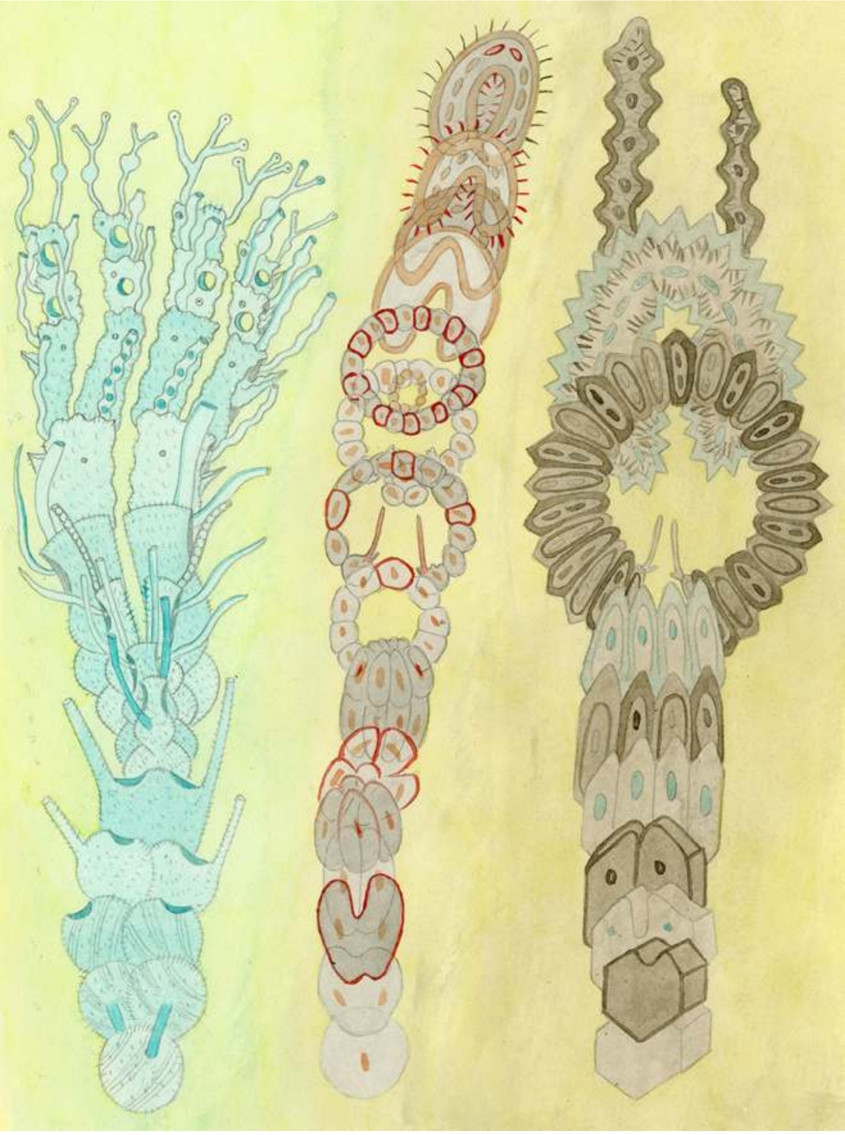


FIGURE 5.2: Gemma Anderson-Tempini, 'Isomorphogenesis no. 1'. Pencil and watercolour on paper, 2014.

the activity of drawing and the facilitation of detailed measurement of aspects of biological phenomena, we argue that the decline of exploratory imagination, and drawing, as part of the scientific process limits the richness of hypothesis formation and, therefore, potential knowledge advancement.

The original purpose of the trans-disciplinary project we describe in this chapter was two-fold: to explore the potential of re-incorporating drawing into a scientific method to provide new insights into this process and to generate images that can convey the dynamic nature of cell division. The outcome was a series of images very different from those found in textbooks, and discussions within the project and feedback from external experts suggest that the new images can, indeed, provide genuine insights into cell division. Moreover, the process of exploring how to represent mitosis itself – the interactions in time and space between the protagonists – serves as an example of how trans-disciplinary research can unfold and contribute to new knowledge and understanding.

Initial explorations

After meeting at a workshop on process biology, Gemma and James began to develop ideas as to how they could use mitosis and cell division as a focus for exploring the potential of drawing in scientific practice. As an initial foray, Gemma asked James to imagine mitosis as a series of verbs based on his understanding of the dynamic interplay between the different sub-cellular elements involved in mitosis – predominantly the protein fibres, the microtubules and the genetic material, DNA.

Building on her isomorphogenesis method Gemma was curious to see if it was possible to generate drawings based on verbs associated with the specific process of mitosis. The following text is from an e-mail sent by Gemma to James.

> 8/06/16
> Dear James,
> Here is an example of verbs used in one Isomorphogenesis artwork:
> Isomorphogenesis no.1
> Three columns –
>
> LEFT: (sphere/multiply+rod/scoop/vertical shoot/merge/twist/tendril extend-divide/bulge+expand/crimp walls/beak/ divide/add nucleus/ change topology/branch/ pod/hairs END) – left series is made following the formsynth drawing system.
>
> MIDDLE: (sphere+nucleus/dent, start divide/partial divide/ contact divide/ contact divide, double, multiply x2/ partial separation/ double up, multiply x2/ segment into circle form/ tendril extend+ add segment/ create inner circle, add self-similar parts- fractalize/ merge, begin divide-upward side/ thicken walls/ add inner nucleus/ add hair, spines END).
>
> RIGHT: (hexagonal prism/begin downward divide/ further divide, add nucleus/ contact divide/ divide again, multiply/ inner circle/ double up/ circulate, add segments/ add tendril extend/ crimp walls/ de-segment, merge/ divide END).
>
> If you could send verbs that you think of specifically for mitosis and meiosis – eg. twist, divide, swap, anything like that. Thanks!

James replied as follows:

> 14/06/16
> Dear Gemma,
> Below is a list of verbs. I've ordered them in terms of time and related them to either microtubules (MT)s, chromosomes, or both, to try to guide your understanding. I sat in a quiet room and imagined the process unfolding, it turned out to be quite sensual. Have fun!
> Tense, go!, burst (MTs), grow (MTs), expand/shrink (MTs), nucleate/birth (MTs), wave (MTs), explore (MTs), probe (MTs), speckle (MTs), offshoot (MTs), align (MTs), bundle (MTs), slide (MTs), coalesce (MTs), focus (MTs), flux (MTs), flow (MTs), mirror (MTs), condense (chromosomes), inhale (chromosomes), tight (chromosomes), touch (MTs and chromosomes), kiss (MTs and chromosomes, join (MTs and chromosomes), co-ordinate (MTs and chromosomes), dance (MTs and chromosomes), align (MTs and chromosomes), balance (MTs and chromosomes), separate (MTs and chromosomes), climax (MTs and chromosomes), expend (MTs and chromosomes), cleave (chromosomes), shorten (MTs), echo (MTs), final pulse (MTs), exhale (chromosomes), relax (chromosomes), decondense (chromosomes), satisfied, rest

Based on this interaction Gemma created two drawings, aiming to visualize the whole process of mitosis in one image (Figures 5.3 and 5.4).

Submerging into science: Summer 2017

As we embarked on 'Representing Biology as Process', Gemma attempted to achieve a greater personal understanding of the process of mitosis by integrating into James's research group for a few months, in particular by reading published research material, viewing open access timelapse movies, listening to scientific presentations during regular lab meetings and shadowing researchers undertaking experimental microscopy of mitosis. Although this was worthwhile, Gemma concluded that an intuitive understanding of the process (necessary for drawing) would not be achieved through such conventional research training that relies on codification and scientific language.

The Drawing Labs

After joining the routine scientific activities of the Wakefield lab, Gemma felt compelled to create a meeting format with the scientists in which drawing would be used to explore ideas and transcend the limits of interdisciplinary communication.

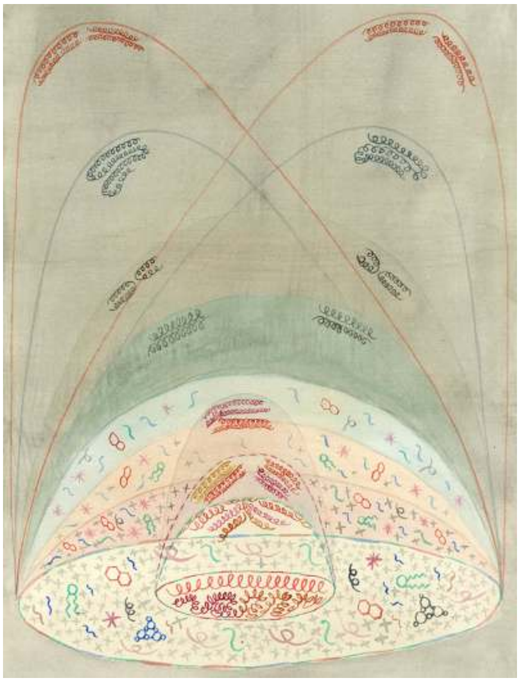


FIGURE 5.3: Gemma Anderson-Tempini, ‘Imagining Mitosis 1’ (series, no. 1). Pencil and watercolour on paper, 2016.

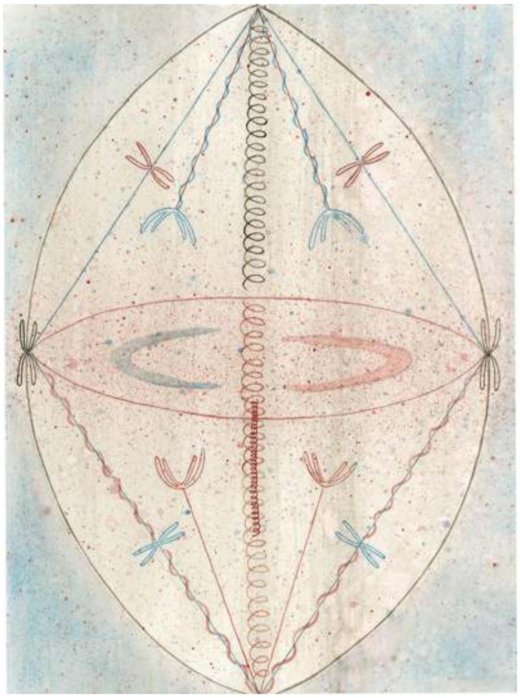


FIGURE 5.4: Gemma Anderson-Tempini, ‘Imagining Mitosis 2’ (series, no. 2). Pencil and watercolour on paper, 2016.

Here we recall the iterative and experimental nature of our attempts to reactivate exploratory imagination as a part of scientific understanding. We began drawing by undertaking a series of collaborative Drawing Labs focused on mitosis. Gemma's intention was to encourage the scientific researchers to use drawing to explore the scope and limits of their knowledge while she would simultaneously learn about cell division. These group activities reintroduced drawing into scientific practice in a supportive though challenging environment, which promoted the refinement and development of ideas through an iterative loop between artists and scientists. To guide each Drawing Lab, Gemma prepared a theme, set of questions and images from which each session could adapt and depart as questions and drawings developed. Over the space of three months (2017–18), Gemma ran five Drawing Labs with the Wakefield group in a large, open-plan workspace within a multidisciplinary research environment (Living Systems Institute, University of Exeter).

Drawing Lab 1: Understanding the participants

The aim of the first session was '*to use drawing to develop understanding of mitosis and to share this understanding*'. Participants were encouraged to '*draw what you know and find out what you don't know*'. To begin with, Gemma led a short visualization exercise for focusing on imagination while ignoring external sensory distractions in order to turn the attention inwards and build mental pictures through a kind of 'inverse vision' (Anderson-Tempini 2017; Anderson-Tempini et al. 2015). Participants selected from a variety of drawing materials provided and either sat alone at a table or shared a table with one other person, to allow individual interpretations to crystallize. The disparity between drawings of mitosis by scientists who work in the same lab prompted a discussion of the possibility of achieving an image consensus within the lab. The results, however, mostly revolved around classical, physical representations (Figure 5.5A).

Drawing Lab 2: Expanding the imagination

The objective of the second session was to enhance the group's perception of the processes within mitosis in order to generate a consensus and to move towards producing a connected space–time image[2] of mitosis that Gemma could then transform into art. To guide the researchers, Gemma asked the group to consider form patterns (or 'omnipresent morphologies'), such as the relationship between monomers and polymers. This time, participants were given a more directed drawing brief: '*to imagine and draw a number of "stages" of mitosis; perhaps 10–15*'. Classically, mitosis is described as a series of five or six quasi-steps (see Figure 5.1). The intention behind expanding this to approximately fifteen steps was to heighten the perception of mitosis as a continuous process and to explore which stages different individual researchers regard as important. In subsequently showing, discussing and refining the different drawings, the collective aim was to find a consensus about the stages with a view to generating a connected space–time

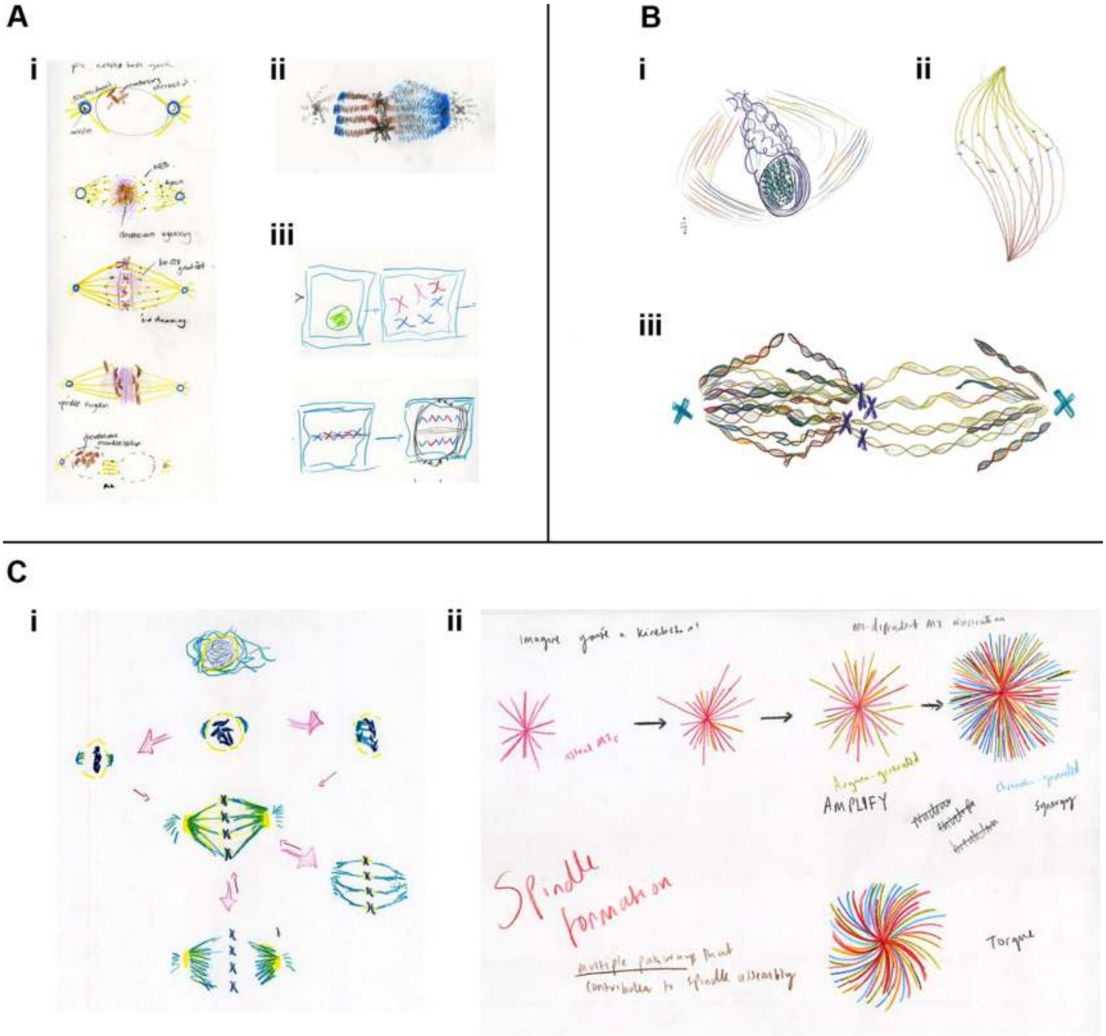


FIGURE 5.5A–C: Examples of drawings from the Drawing Labs. (A) Results from session one. (i) Ph.D. student drawing of stages of mitosis. (ii) Researcher drawing of the mitotic spindle, emphasizing differences between kinetochore microtubules (left) and spindle microtubules (right). (iii) Researcher drawing of stages of mitosis. (B) Results from session two. (i) Researcher drawing, imagining the spindle from an alternative perspective. (ii) Gemma Anderson-Tempini (artist) drawing mitotic spindle, emphasizing chirality. (iii) Researcher drawing of metaphase, emphasizing the helical nature of microtubules, emanating from the centrosome (right), and from both the centrosome and the chromosomes (left). (C) Results from session three. (i) Researcher drawing, with arrows reflecting the many possibilities associated with mitosis. (ii) Ph.D. student drawing of mitotic microtubule generation. Words, colours and shapes combine to accentuate relationships in time and space and between the forces acting upon and within the spindle.

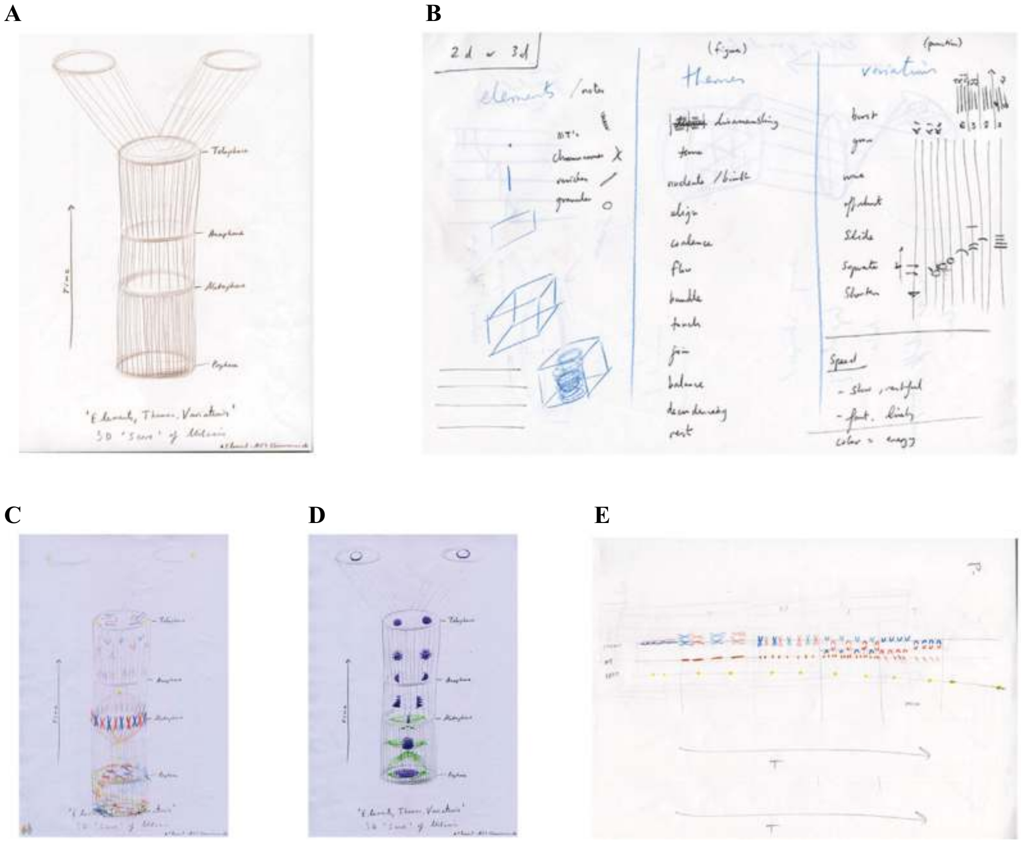


FIGURE 5.6A–E: The score template and initial exploratory drawings. (A) Gemma Anderson-Tempini, drawing of a 4D (3D plus time) score template for session four. (B) Gemma Anderson-Tempini, sketch of the contents for the flow system: elements of mitosis, choreographic and musical terms and verbs. (C, D) Ph.D. student drawings of 'polyphony' of mitosis elements within the 4D score template. (E) Ph.D. student drawing of the 2D score template.

image of mitosis. A recent article describing an intrinsic chirality within the mitotic spindle, identified by one researcher, influenced some drawings (Novak et al. 2018), which consequently reflected a more open and creative interpretation of spindle formation (Figure 5.5).

Drawing Lab 3: Archetypes, applications and inspiration

The third session moved further towards a 'processual view' by introducing selected words and theoretical concepts as guides and catalysts for drawing. Returning to the 'mitosis verbs'[3] based on the isomorphogenesis[4] approach, this session revolved around the question '*Is it possible to create a model of mitosis through drawing?*' The rationale for this was to attempt to facilitate drawings that would reflect the salient underlying principles of mitosis. After discussing with James dynamical systems theory and the work of theoretical biologists such as Waddington, Goodwin and Kauffman, Gemma introduced contextual 'systems' concepts, including flow systems,[5] parameters, limitations, attractor points and landscapes. The group was then invited to think about 'primitive' or archetypal forms, or to imagine a time slice of mitosis, along with the potentialities that arise as each progressive 'snapshot' opens up a variety of 'adjacent possible' future pathways (revealing 'n' pathways/directions), leading to different cellular outcomes. James prefaced his participation by drawing on a board a variety of spindle types based on a single 'Urpe-spindle', drawing inspiration from Goethe's work on plant morphology and the concept of the 'Urpe-Pflanze'. Gemma followed by drawing on another board images to emphasize parameters and directional flow and suggested that the group consider thinking backwards to imagine the historical moves towards the time-slice and to think of the trajectory as having many possible directions[6] (see Figures 4.10 and 4.11).

> If I look at the created object, inquire into its creation, and follow this process back as far as I can, I will find a series of steps. Since these are not actually seen together before me, I must visualize them in my memory so that they form a certain ideal whole. At first I will tend to think in terms of steps, but nature leaves no gaps, and thus in the end, I will have to see this progression of uninterrupted activity as a whole. I can do so by dissolving the particular without destroying the impression itself.
>
> (Goethe 1996: n.pag.)

To emphasize the many possible routes to spindle formation, and the consequent fates of these mitoses, the group were encouraged to imagine and then articulate how a 'normal' series of mitosis images might differ from a pathological image, such as seen in cancer cells. The drawings that emerged were very interesting: one researcher, who drew mitosis with different outcomes at each stage, was asked by Gemma if pathological stages could re-join the 'normal' stages at any point and then she drew new arrows to indicate that stages could be 'rescued' and return to 'normal'. This seemed interesting as this is generally not represented in textbooks. In this Drawing Lab, drawings moved further away from concern with mimicking appearances and representing what is seen optically and towards imagining the process, using the drawing process to imagine *being like* the stages, dynamics and elements of the process itself. The process of drawing takes on a performative role of *becoming* and reifying the process of mitosis.

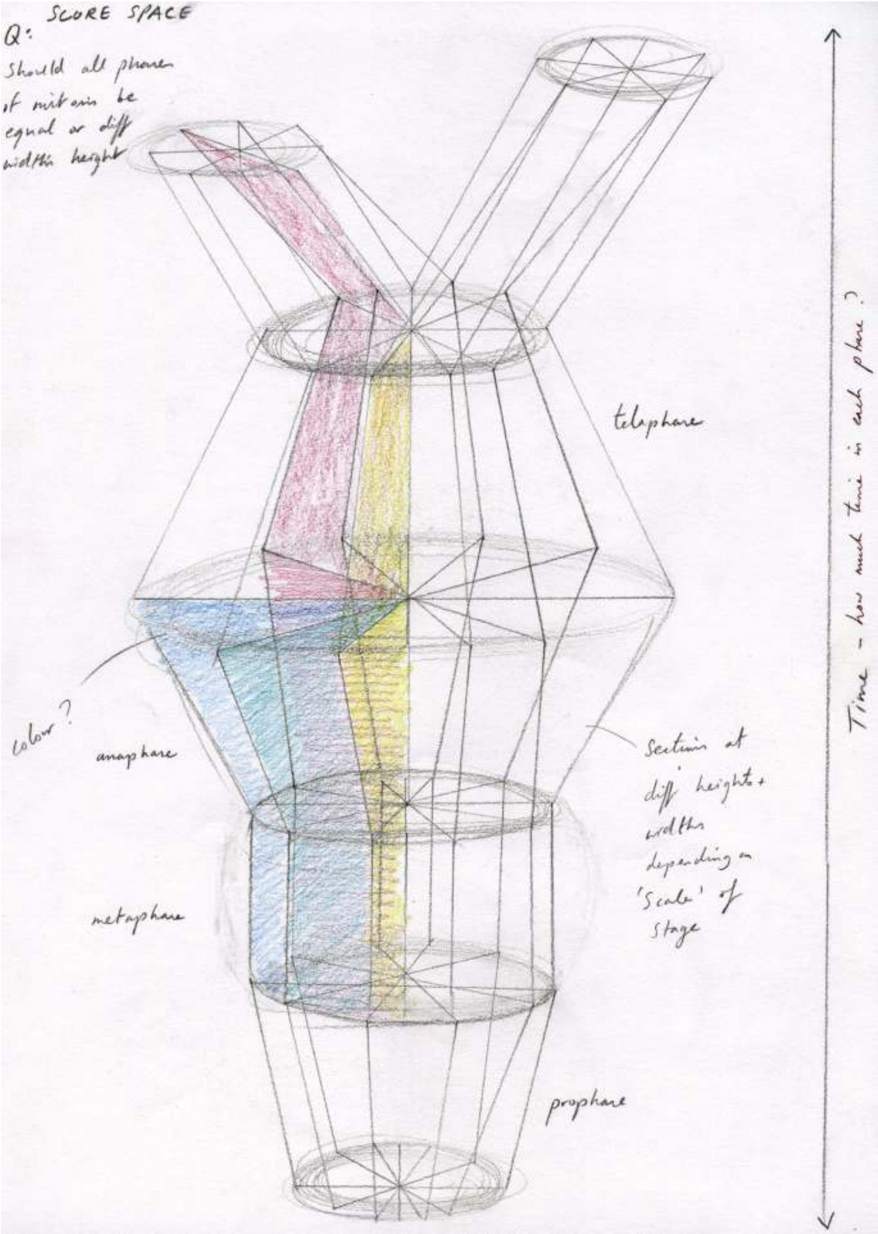


FIGURE 5.7: Gemma Anderson-Tempini, ‘Drawing of abstract structure of mitosis’ as template for Drawing Labs, 2017.

Drawing Lab 4: Finding a common imaginative language in choreography

As the first three sessions underscored the challenge of breaking away from traditional, structure-based representations of mitosis, we searched for analogies and concepts that would encourage more dynamic drawing. Drawing on choreographic principles and musical analogies, Gemma introduced the theme of the ‘score’ into the fourth session. The spatio-temporal interactions between DNA and microtubules during cell division are often described as a ‘dance’ (Yang and Yu 2018; Klutstein and Cooper 2014; Gough 2011; Stukenberg and Foltz 2010; Munro 2007), while in choreography, music or art a score is a set of guides or cues that are interpreted by multiple elements (individuals, instruments) through time. Moreover, musical analogies have figured in several attempts to rethink biological ideas, such as the genome as a jazz score, or more general metaphors of life as music (Porta 2003; Noble 2008). As a tool for imagining, artists have long been interested in the ‘score’ as a scaffold and constraint for creative work. In the work of Fluxist artists and John Cage, for example, we find multiple definitions of ‘score’.[7] Similarly, different musical notations exhibit different degrees of abstraction. For example, standard staff notation is a very abstract way of writing a score, as all the relations between notation and sound are defined by conventions. Various forms of tablature provide a partly iconic representation of the pattern of fingers stopping the strings to be sounded. The standard representation of guitar chords is highly iconic. The tablature of other instruments is less so; lines represent the strings quite literally and are therefore wholly conventional representations. ‘Choreography is always about translating, about going from one state to the other, or from idea to thing, or idea to action […] it is the force of an idea that pushes people into action’ (Forsythe 2003: n.pag.).

If we consider understanding biological process to be about understanding spatial/temporal relationships between activities that result in emergent phenomena, then choreography as ‘an organizational practice’ seems suitable as a heuristic. Both choreography and music are movement practices within a temporal framework that instrumentalize different bodies (i.e. the instrument of choreography is generally the human body, and the instrument of music is generally the musical instrument activated by the human body). Similarly, the chromosomes (the DNA), the microtubules and the cell membrane can be construed as the instruments of mitosis, and as subject to composition in a score.

To provide drawing lab participants with a score framework for their work, Gemma sought a physical template that could be used to guide the individual imaginings. From learning the harp, she remembered that musical notation can be read both horizontally (following the conventions of the western reading style) and vertically (like a waterfall).[8] Therefore, for the fourth session, Gemma drew a 3D score in time (4D) that was to be read vertically (height = time).[9] Participants soon noticed that this score template possessed similarities to a widely used convention for visualizing spatio-temporal cell biology images taken using microscopes, termed a ‘kymograph’ (a device that draws a graphical representation of spatial position over time in which one spatial axis represents time; Figure 5.1; Hayward et al. 2014) (Figure 5.3). As the group began drawing mitosis onto the score, the benefit of this structure became immediately apparent. One lab member immediately drew a kind of polyphony (image), which was then revised into a more abstract and relational image; another described their first attempt as 'where all the mistakes were made' and then made a second attempt that strongly invited a musical reading (Figure 5.6A–E). The score template, therefore, provided a framework within which participants could explore and draw elements of mitosis to facilitate more exploratory and engaging interactions.

Synthesizing the Drawing Labs: Iterative dialogue

Following these four drawing lab sessions, Gemma and James began a dialogue with the aim of developing the individual scores into a synthesized single representation of mitosis. Aware that the 'score' had an arbitrary tube-like shape, Gemma prefaced the first dialogue by asking '*what shape does the process body of mitosis take?*' This proved crucial to the project. As James's research focuses on how different microtubule-generating pathways contribute to mitotic spindle formation in fruit fly (*Drosophila*) embryos, we initially focused on replacing the physical representations of microtubules. James began to articulate journeys of the microtubules from entry into mitosis, through chromosome alignment in the centre of the cell, to chromosome segregation, through verbal description and physical gesture. Together, Gemma and James sketched these 'waxings and wanings' of microtubule activities onto the score template, thus transforming the tube into something with added dimensionality, where mitosis starts at the bottom of the drawing and ends at the top. Iterative re-imagining and re-describing of these activities – or energy flows – over time led to the co-creation of the first 'mitosis score' (Figure 5.8A) drawing for microtubules.

The score was then filled with colours and shapes corresponding to different physical elements of mitosis. In fruit fly mitosis, the microtubules are generated in three distinct sub-processes – through nucleating centres termed centrosomes, nucleation at the chromosomes and microtubule-dependent amplification (branching microtubule nucleation). Each activity was shaded in a different colour within the constraints of the score (red, purple and green, respectively). Physical representations of chromosomes (blue) were retained by representing their condensation, movement to the metaphase plate, segregation and decondensation, alongside a representation of kinetochores (the protein links present on chromosomes which attach to the spindle microtubules) and the forces acting upon these entities (orange circles and bars, where the forces applied to individual kinetochores within a pair are represented by the thickness of the bar).

Drawing Lab 5: Seeking consensus – Initial validation and further experiments with the mitosis score

Scientific practice seeks consensus. Whereas traditional experiments focus on repeatable phenomena, we sought consensus by presenting and explaining the 'mitosis score' drawing to the Wakefield Lab. We discussed the elements and agreed to work collaboratively, with each participant 'becoming' a different element of mitosis (i.e. microtubules, chromosome, etc.). The emphasis was on drawing not to illustrate but to resemble and to 'be like' mitosis. First, we drew general pathways and then elements moving along pathways (after watching 'Dots' animation by Norman McLaren for inspiration) and we thought of varieties of 'conventions' or signs for each element. The value of this session lay in validating the concept of the score; at this point, everyone in the lab understood that it communicated something about mitosis.

Applications of the initial mitosis score to other types of cell division

Following the Drawing Labs, Gemma and James met on further occasions to explore, create and revise drawings. We found that the principles – or the core concept – of the *Drosophila* mitotic microtubule score, and its contents, could be easily applied to other mitoses, where the precise dynamics of spindle formation and chromosome segregation, and the contributions of each of the different microtubule-generating pathways differ. Data pertaining to particular mitoses – both interpreted and imagined – were used to create drawings of mitosis in a human tissue culture cell (Figure 5.8B), two imagined dysregulated (cancer) human cells (Figure 5.8C and D), plant cells and fission yeast (Figure 5.8E and F). We discussed to what extent the shapes and features are intuitive and imaginary, and to what extent they are based on quantifiable data. We were also interested in the relationship between codification and intuition in the image.

Reducing the 'physicality' of the mitosis score: extending the imaginative principle to create the final archetypal mitosis score.

When the scores in Figure 5.8 were drawn, it was unclear what the overall sculpted shape of the mitosis score related to, besides a dynamic perspective on the organization of microtubules. Gemma and James then began to discretize the score further, by adding conventions to visually code the dynamics within the score and discussing the transformation of the organelles/Golgi apparatus in relation to

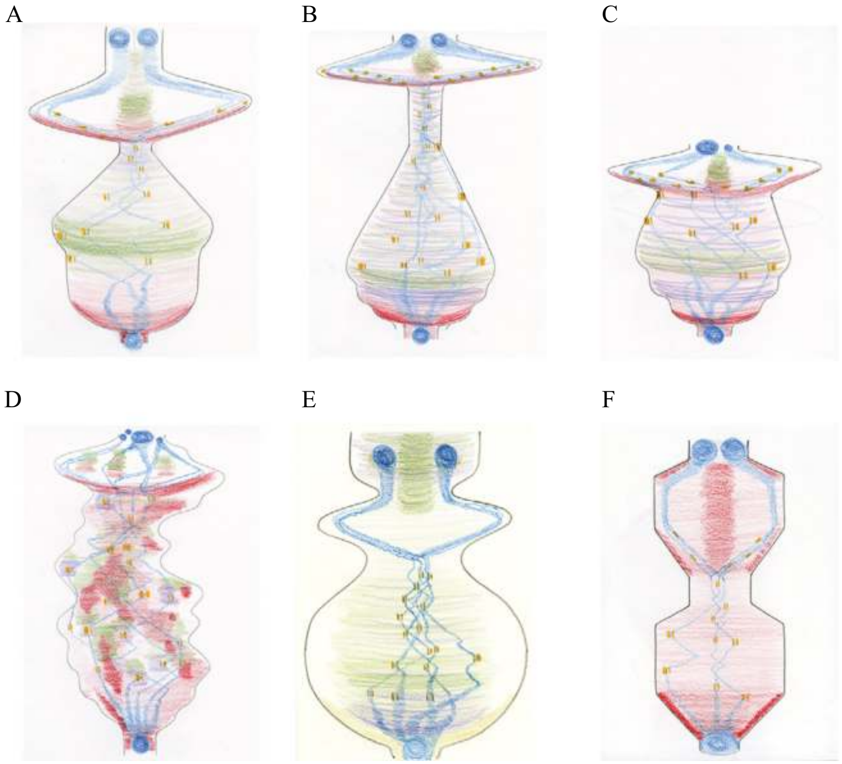


FIGURE 5.8A–F: (A) Mitosis in a *Drosophila* embryo over time. The overall shape directly corresponds to the sum of the spindle/microtubule-generating pathways and their interactions with chromosomes. As mitosis starts, there is a large burst of microtubule nucleation from the centrosomes, roughly coincidental with the condensation of chromosomes. A full mitotic spindle forms, supplemented by augmin-dependent microtubules. Chromosome congression happens quickly as the microtubule-generating pathways reach a steady state. After a very brief spindle assembly checkpoint, the segregation of chromosomes ensues, driven by microtubule depolymerization. A population of microtubules, originally generated by centrosomes and supplemented by augmin-generated microtubules, form the central spindle required to keep the decondensing chromosomes/reforming nuclei apart. (B) Mitosis in a human tissue culture cell. The same principles as (A) apply. The extended 'body' reflects the greater time needed to align chromosomes (23 pairs instead of the four pairs in *Drosophila*) and the increased time between metaphase and anaphase (about twenty minutes in humans, compared to about one minute in *Drosophila*). Chromatin-dependent microtubule generation is visible due to the extended time required for chromosome alignment. (C) Abnormal mitosis in a human cell lacking the spindle assembly checkpoint (shown by the truncated shape), which results in abnormal chromosome segregation and the generation of nuclei of different sizes. (D) Abnormal mitosis in a human cell with a defective spindle stability, which causes ongoing spindle rebooting and the production of an unstable protein mass. (E) Mitosis in a plant cell. As centrosomes are absent in higher plant cells, the formation of microtubules is facilitated predominantly by chromatin and by the nuclear envelope, and amplified by augmin-dependent microtubules. (F) Mitosis in fission yeast demonstrating a closed mitosis and a bar-like mitotic spindle, generated purely from spindle pole body-nucleated microtubules. Both spindle formation and anaphase are intuited as 'ratchet-like' and measured, rather than explosive.

stages of mitosis. However, this increased 'codification' of more 'things' interacting during mitosis led to confusion and to questions about the spatial nature of the 'diagram'. Gemma asked James about the drawn, but arbitrary, pathways of the chromosomes. As they can take infinitely many paths, it seemed strange that DNA was given specific paths in the image. The process of making the images was highly iterative; Gemma made drawings that included questions (Figure 5.9) for feedback in meetings but also sent them to the Wakefield lab via email and the online collaborative platform, Slack. These drawings then informed further artworks.[10] experimenting with the new forms.

These iterations led us to the conclusion that the shape of the score was actually related to the energy inherent in and being applied by the microtubule system during mitosis. This revelation opened up myriad possibilities and a framework to apply to the previously codified chromosomes. We were now looking at mitosis as a transformation of the cell, inseparable from the cell: the process does not happen 'on' the score; the score is not empty; rather, the process is the score and the score is the process. Instead of more, we now began to make the score less discretized. We saw that the score we had before was the spindle score, and in fact, there were other scores in the pictures. James began to draw 'scores within scores' using the principles of the microtubule score: energy is required to both condense chromosomes at the start of mitosis and to decondense them following segregation, whilst additional input is needed to nucleate microtubules around the chromosomes and, through kinetochores, to assist their alignment. Thus, a score could be drawn for the DNA. This principle was then extended to the cell cortex (i.e. the forces acting on the cell membrane), where the rounding of the cell prior to mitosis, cytokinesis and the re-shaping of the cell following division provided a corresponding energy-related shape. This allowed the mitosis scores to be extended to include the terminal stage – cytokinesis (or cell splitting).[11] We also saw the gaps between scores – the non-scores that are devoid of energy; the positive and negative space of mitosis; the activity and passivity in the process and the interactions between individual energy landscapes – the layers of energy landscapes and the overlapping transformations that led to cytokinesis.

James and Gemma met a final time to complete the picture, to draw the individual energy landscapes in relation to one another – i.e. of microtubules, DNA and cell cortex – and to encapsulate them in an enveloping score. Unconventional colours (e.g. purple for microtubules, yellow for chromosomes and brown for the cell cortex) were chosen to liberate the shapes from preconceived and widely used conventions. The aim was to draw everything together, to obtain closure (or a phase of resting) after the dynamicity associated with the explorative drawing process and to consider the relationship between the passive and

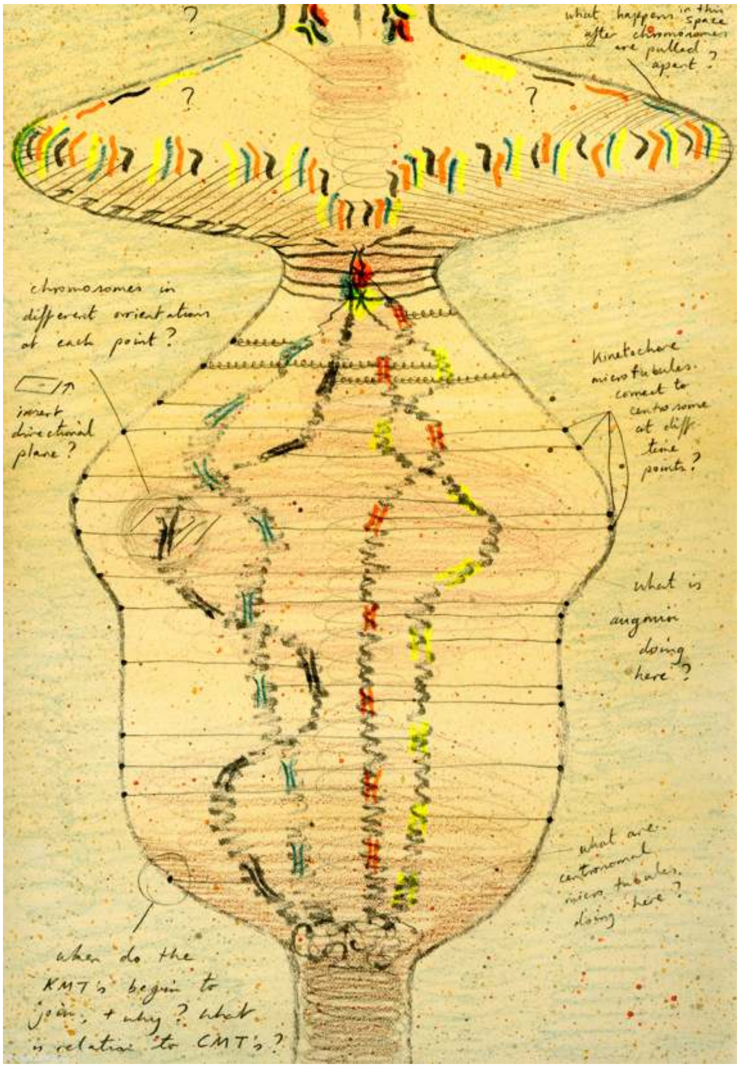


FIGURE 5.9: Gemma Anderson-Tempini, ‘Mitosis?’ Pencil and watercolour on paper, 2018.

the active throughout the cell during mitosis. Quiet reflection post-drawing led to some new and holistic insights and thoughts on the process of cell division, as exemplified by this e-mail sent by James to Gemma shortly after the process concluded.

E-mail from James (February 2019):

> *I’ve been quietly contemplating the final cell division drawing. I am finding it quite awe inspiring and full of fresh meaning. Whether this is meaning I am placing on it due to the human capacity to find connections, or whether there is a deeper sense in which it is ‘right’, I don’t know.*

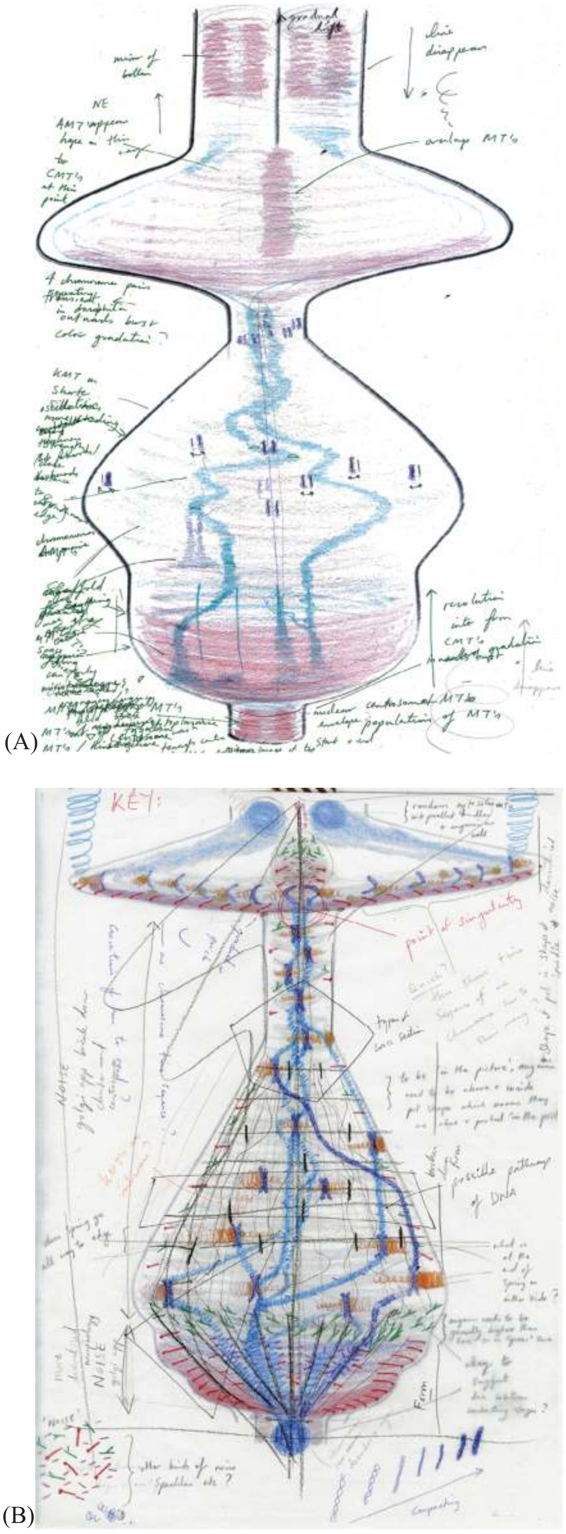


FIGURE 5.10A and B: Gemma Anderson-Tempini, ‘Mitosis working drawing’. Pencil and watercolour on paper, 2018.

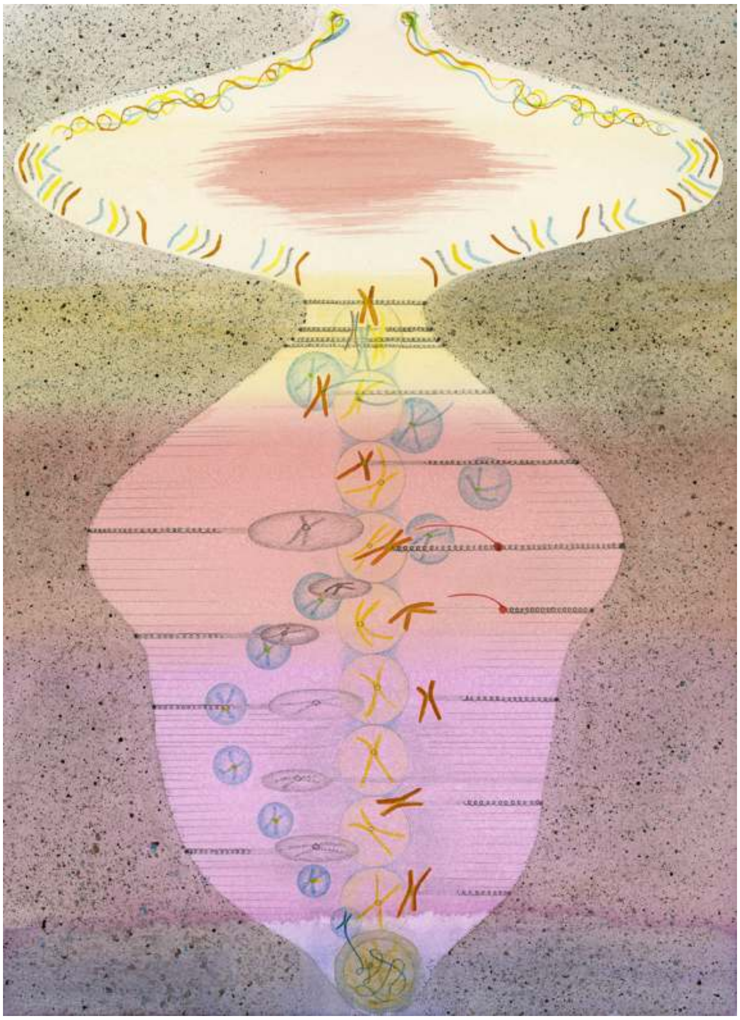


FIGURE 5.11: Gemma Anderson-Tempini, ‘Garden of Forking Paths; Mitosis Score no. 5’. Pencil, watercolour and colour pencil on paper, 31 × 41 cm, 2019.

> *It has a poise and regality to it that seems somehow ethereal […]. You can see within it the biological, animal form – with the symmetry, the rhythm and the flow of the lines representing the arms and the torso. And once you have that, you notice that the centre point of activity in the lower half rests within the ‘womb’. And what is that womb, biologically speaking? It’s the DNA being held, cradle-like, by the mitotic spindle. So you have the essence of life – the biological universality of replicated nucleic acid, carrying the potential to render life through division – in a cradle-like organisation of fibres, cosseting it, protecting it and holding it. And then to anaphase, where the arms (literally) are pulling the two genomes apart, quickly but with a security and depth provided by the safety of the cortex.*

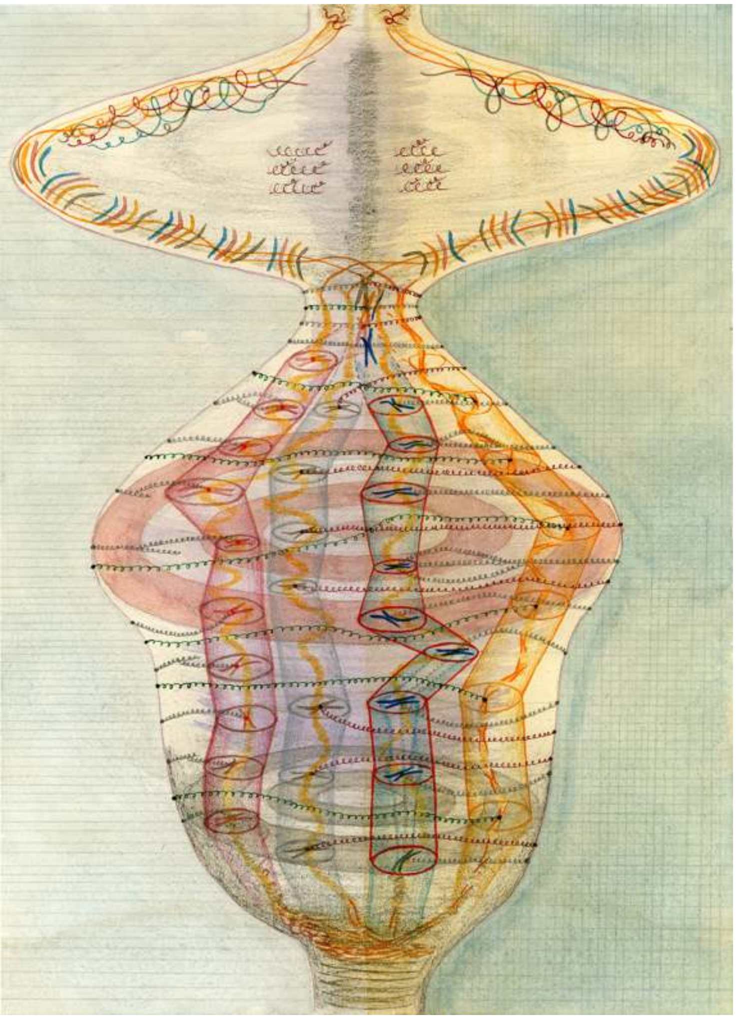


FIGURE 5.12: Gemma Anderson-Tempini, ‘Garden of Forking Paths; Mitosis Score no. 6’. Pencil, watercolour and colour pencil on paper, 31 × 41 cm, 2019.

Testing the representation within the scientific community

To see whether the scores held ‘truth’, i.e., whether they could be recognized as being related to the physical entities, activities and sub-processes of cell division, we sent the drawings to four senior scientists in the field, each with over 25 years of experience. They were asked to describe their thoughts and feelings before they were provided with a series of keywords and, finally, explanations of the drawings (Anderson-Tempini et al. 2019; Supplementary data). With only the final score (Figure 5.7) to look at, there was little to orient the experts. However, two asked whether the drawing was a kymograph, and one suggested that ‘the purple or yellow represents separating chromosomes or spindle poles’.

Providing the experts with initial keywords (kymograph and energy potential) elicited some very detailed responses in which the major elements of the pictures were correctly identified. Moreover, once the mitosis scores containing the physical representations of the blue chromosomes were shown, a majority of the experts were able to discern the key and relate the pictures to different types of mitosis (Anderson-Tempini et al. 2019; Supplementary data). From these responses, we conclude that our new representation of cell division has value in conveying something of its dynamic nature, in relation to key activities that contribute to it – at least to those familiar with the central concepts. We, therefore, believe that the representation could be a useful communicator of knowledge about processes in a pedagogic context.

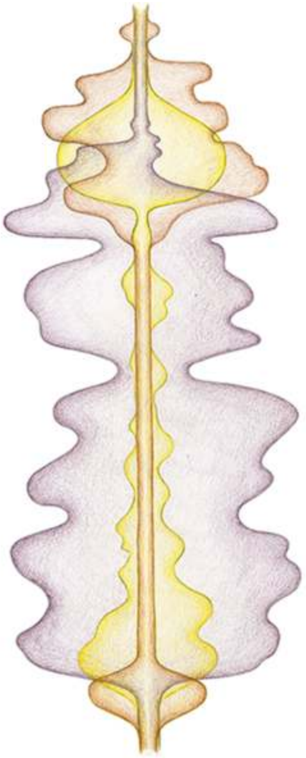
The processual representation of cell division as a hypothesis generator

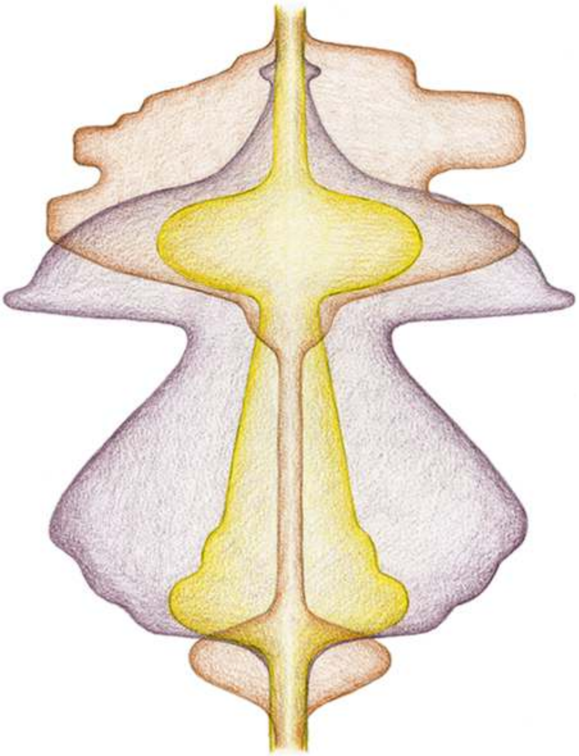
One central aim of this project was to explore whether dynamic representations such as ours could be collaboratively created with, and used by, scientists to generate new, testable hypotheses (always drawing on their existing knowledge and intuition). Reflections by the researchers on the final score not only suggested analogies with other life processes (Supplementary file 4) but also brought to the fore a number of questions about the process of cell division.

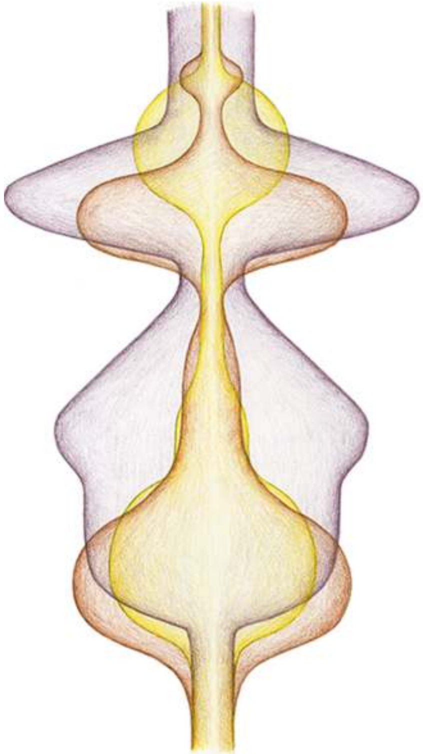
For example, what sub-cellular activities apart from the microtubules, DNA and cell cortex are not represented by the score? How would its shape change when other elements, such as the endomembrane system, are incorporated? Does the narrowing of the shape during metaphase reflect omitted activities, such as the poleward flux of microtubules (the continuous shortening and lengthening of the microtubules that

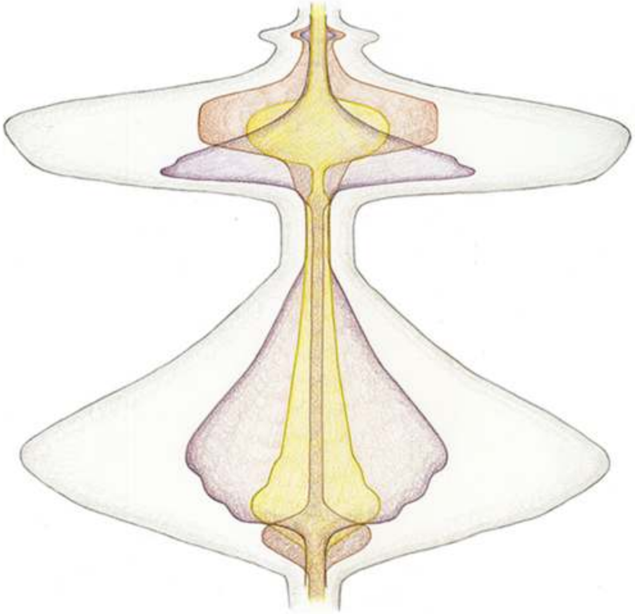
FIGURE 5.13: A new dynamic representation of cell division in different states. Cell division, beginning at the transition from the G2 phase of the cell cycle to mitosis (bottom) and finishing after cytokinesis when the cells divide (top). The energies related to the input of microtubule-generating pathways are now combined in purple, with chromosome-related processes in yellow and activities related to the cell cortex/membrane in brown. Just before mitosis starts, the cell actively rounds up. Then, during prophase, the microtubules nucleate the chromosomes condense and are moved within the spindle. As chromosome alignment proceeds from prometaphase to metaphase, microtubules and chromosomes reach a steady state – hence the narrowing of the corresponding shapes. The activity of microtubules dramatically increases early in anaphase, which helps to segregate the chromosomes, which are just 'passive passengers'. By late anaphase, however, the decondensation of the chromosomes begins at the same time as the cortical acto-myosin contractile ring forms and contracts. Finally, cytokinesis itself occurs, requiring a small coordinated input from microtubules and the cell cortex. The outer grey shape represents the combined input of each activity described above – therefore corresponding to the overall energy/level of activity of cell division.

(Continued)









do not affect the shape or size of the spindle, but that causes energy to flow from the centre of the spindle to the poles)? Or does the cell's energetic input into mitosis change over time? If so, what is the relationship between microtubule dynamics and mitochondria, the energy providers of the cell? Further, given that the mitochondria produce adenosine triphosphate, while the energy source of microtubule dynamics is guanosine triphosphate (GTP), how is the exchange of energy type accomplished? Where are the proteins that do this, and when do they do this?

These questions are new to the scientist involved in this project, even after twenty years of research. As such, the scores provide a rich source of ideas for future experiments. Similarly, new questions are raised for artistic practice. For example, how should we imagine the repetition and variation of countless iterations of cell division? How can we represent time within a 2D framework? And how do we draw cell division as a process within processes that are intersecting and interconnecting?

Relational process drawings and process-based diagramming

We have developed a new approach to the depiction of natural history through 'relational process drawings'. Rather than focusing on the morphology of the *object*, our drawings focus on the dynamic patterns of the processes of life and draw together relationships between energy, time, movement and environment at the molecular, cellular and organismal scale.

The process of mitosis (cell division) – drawn here in collaboration with biologist James Wakefield – is co-dependent with and nested in other processes: protein folding is essential to cell division, which is essential to the development of the embryo (embryogenesis). Each process is intrinsically and reciprocally related to many others. The artistic view of this delicate, beyond visible, dynamic procedure allows us to explore the entire process of cell division in one connected image and to think of it in unconventional terms, that is, as a dance, a score, an energetic form.

Although they are not intended as realistic depictions, as 'diagrams' the mitosis score images can and often do reflect real properties of the biological process under investigation (cell division). The drawings with notations (Figure 5.14A–C) are a kind of *hybrid* representation, in that they combine, to varying degrees, visual, numerical and linguistic expressions (Anderson-Tempini 2021). Whereas the later drawings are composed of visual representations only (Figure 5.13), as we no longer needed writing to clarify what we were doing; the process of drawing itself clarified the image that we held in our minds.

In the notational drawings (Figure 5.14), we guide what the viewer sees with the help of explanatory symbols, linguistic expressions, numerical values and by colouring certain regions so that they also act as a description of the image.

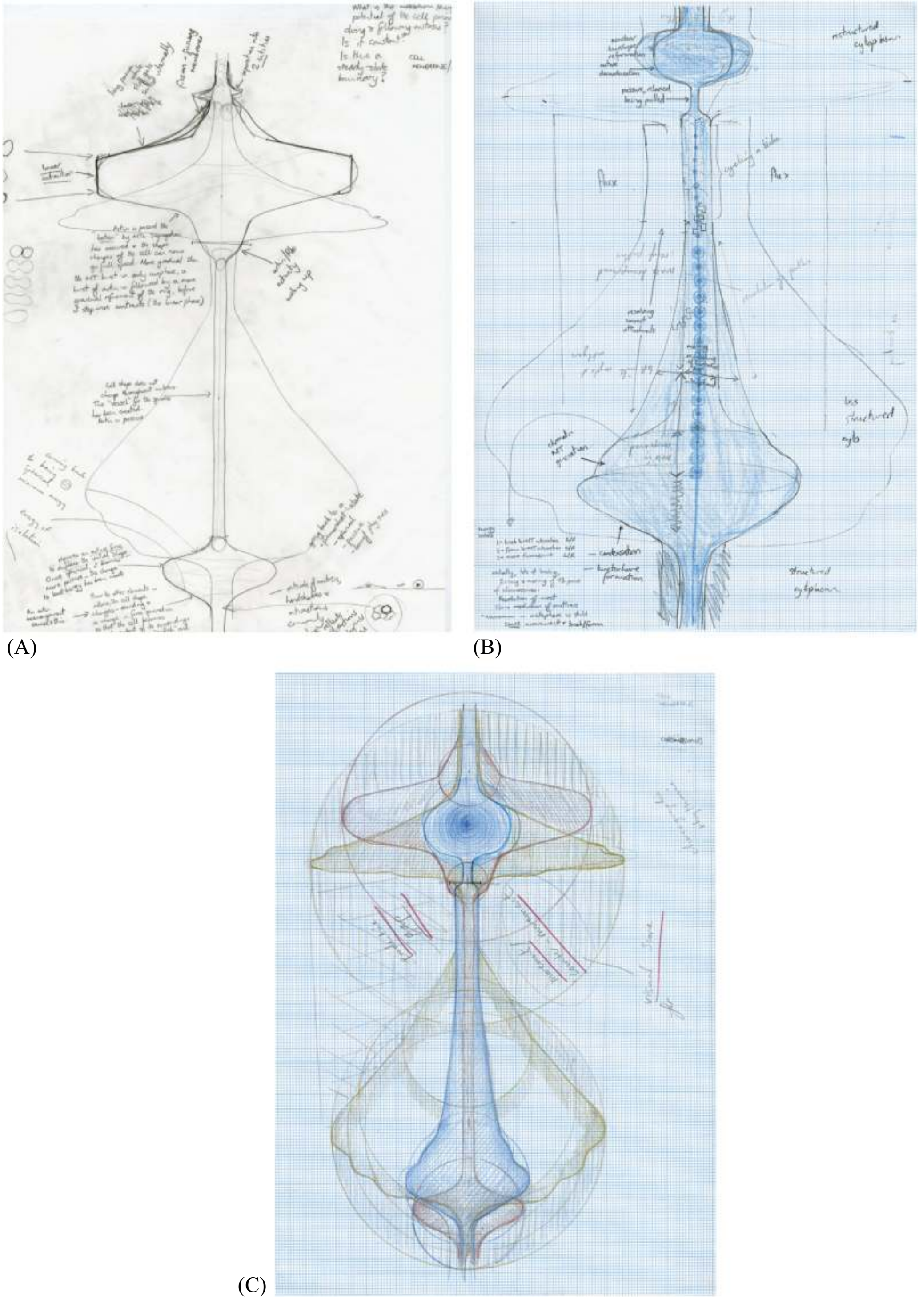


FIGURE 5.14A–C: Gemma Anderson-Tempini and James Wakefield, ‘Garden of forking paths; working drawings’. Pencil and colour pencil on paper, 29.7 × 42 cm, 2019.

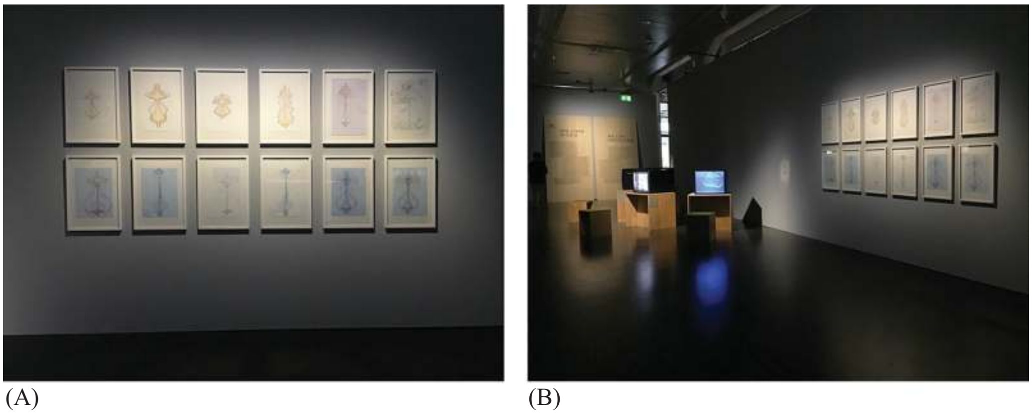

(A) (B)

FIGURE 5.15A–B: Gemma Anderson-Tempini and James Wakefield, 'Garden of forking paths; Mitosis Score'. (A, B) Pencil and colour pencil on paper, 29.7 × 42 cm, 2019. (C, D) Artwork installed as part of the 'Critical Zones' exhibition at ZKM Center for Art and Media, Karlsruhe, Germany.

> Figuring is a way of thinking or cogitating or meditating or hanging out with ideas. I'm interested in how figures help us avoid the deadly fantasy of the literal. Of course, the literal is another trope but we are going to hold the literal still for a minute, as the trope of no trope. Figures help us avoid the fantasy of 'the one true meaning'. They are simultaneously visual and narrative as well as mathematical. They are very sensual.
>
> (Haraway and Kenney 2015: 255–70)

Reflections on the Drawing Lab process

We argue that Drawing Labs can be a tool for sharing and critiquing drawing methods and for engaging different collectives in drawing practices. We found that as a constructive and partially social method of collaboration (between artist and scientist, and between scientists), Drawing Labs enhanced the creativity of the scientific process. We found many ways to draw within Drawing Labs: drawing of, drawing from, drawing with, drawing together, drawing into and drawing out (extracting). And, as a way of understanding biological processes, drawing has the following modalities: drawing to infer – to 'draw hypotheses', drawing not to illustrate but to 'be like' a biological process, drawing to select salient information and drawing to understand and to share this understanding with others. To enable this, it is important to create appropriate conditions for drawing by providing the following questions to guide enquiry, the source material for inspiration, a quiet environment, no personal devices, adequate and quality materials and a tidy and comfortable space. It is also essential to encourage an attitude of open-mindedness, non-judgemental behaviour, patience and curiosity before and during the drawing process.

This approach can be adapted to involve general audiences for purposes of divulgation and participation, and also between lab team members to collaborate and as a way of exchange. Drawing techniques have been developed to provide illuminating and informative representations of the active biological process of mitosis, the subsequent feedback from scientists in the lab reflects on how these techniques can be used as a means of helping to interpret, reflect and theorize mitosis in an interdisciplinary context. Scientists commented that drawing reminded them of the beauty of the process of mitosis and how drawing helped them to develop a more imaginative engagement with mitosis. Some reported that drawing helped to see mitosis as 'a story rather than a snapshot' and to see 'the broader picture' while others commented it was also good to 'consider 4D' (i.e. including time). All agreed that the 'score' structure provided was helpful as it removed the fear that can arise when one starts to draw on a blank page. Further, drawing was considered to be 'quite meditative' allowing 'the brain to clear and reflect', as Petherbridge says 'drawing renders thought visible through its simple tools and unimpeded technique, and functions as the most direct externalization of the conceptual' (Petherbridge 2010: 2). The group also reported enjoying seeing how the interpretative drawings of different lab members differed even though they started from the same set of instructions.

Conclusion: Drawing as a process-centred epistemology

In the case at hand, drawing provides for more engaged access to and reflection on the process of mitosis than 'witnessing' the mechanical generation of biological representations by means of various imaging devices. We suggest that Drawing Labs have the potential to influence the methodological and theoretical approach of the science community.

The difficulty of interpreting the images and the potential rewards of doing so point to further questions and research. Why does the score have the shape it does? Can we tell the cancerous score shape apart from the 'normal' score shape? Is this intuitive? And why is this useful? What is the link between the phenomena and the image? We are also considering lab experiments, such as measuring correlations between energy and aspects of score shape.

Although this project started as an attempt to develop better representations of dynamic phenomena, a somewhat unexpected outcome has been an insight into the dynamic nature of the research process itself. Drawing shifts our focus from the image as a product (an almost inevitable by-product of witnessing biological processes through various imaging devices) to image production as an integral part of the research. The drawing process itself evolves in the course of iterations that generate new questions, challenges and problems, which provide the starting point for the next generation of drawings. This activity, as described in the preceding sections, can generate scientific insight and novel hypotheses. We suspect that these benefits might be even greater when a drawing is integrated into primary research, rather than being used to explore the representation of already established results. In the words of art historian Michael Podro:

> We tend to consider images as subject matter only for visual scrutiny; as external – confronting the mind, as opposed to offering, like language, something in which the mind could participate. The problem for the defenders of images is therefore to show how they could – like language – be internal, open to the mind's participation, part of the mind's own thought and workings.
>
> (Podro 1998: 8)

Artists have long drawn inspiration from scientific images, but here we see the artist co-creating images with scientists and thereby influencing how the phenomena with which they both engage are understood. The process of drawing facilitates a move from reproducing what is seen towards imagining the shape of the biological process being studied. Drawing helps us to explore what lies beyond the bounds of accepted conceptual exploration, to envision the stages, dynamics and elements of which it is composed and perhaps even to adopt an internal viewpoint of what it is *like to be* that phenomenon. The role of drawing in the Drawing Labs is to bring to light phenomena that would otherwise remain latent and to expose 'those confessions of ignorance of the pencil's point' (Hinton 1896: 17). The opportunity to collaboratively explore and develop ideas, to create new representations of living phenomena and to stimulate intellectual decisions about what is included and excluded from such representations gives drawing its unique value as a way of knowing.

ACKNOWLEDGEMENTS

We thank members of the Wakefield lab for participating and enthusiastically engaging with the project, especially the Drawing Labs. We thank Susanne Lens, Maurizio Gatti, Claire Walczak and Rebecca Heald for critically and imaginatively assessing the mitosis and cell division scores, and for allowing their comments to be published. We also thank David Hay and Chiara Ambrosio for helping us to develop ideas along the way.

NOTES

1. This is not a numerical score but a quasi-musical score.
2. Ref influence of embryogenesis drawings.
3. Isomorphogenesis is a series of artworks and an artistic method created by Gemma (Chapter 7; Anderson-Tempini 2017).

4. Isomorphogenesis-based flow system.
5. Taking inspiration from embryo images (Chapter 4).
6. Many fluxus works are designed as scores which can be realized by artists other than the creator. Musicality is linked to experimentalism and the scientific method (ref fluxus catalogue). The score suggests that the same work may be realized several times, and in each state, it may be the same work even though it is a different realization of the work.

   Prose score: a set of instructions, like a recipe.

   Graphic score: pictures and symbols suggest the qualities and characteristics of a sound (energy), such as loudness, duration and timbre. Often used where the music contains extended techniques (unconventional ways of playing instruments).

   Time–space notation: a visual representation of the relationship between the sounds, conveyed by the amount of space they take up on the page. The further apart that sounds appear on the page, the longer the time is taken between them – the closer together they are, the shorter the time.

   Conventional staff notation: a five-line stave and graphic symbols (notes) convey information about pitch and rhythm. It can be thought of as a graph where the Y-axis is pitch (relative height of the note) and the X-axis is time.
7. They can, in fact, be played in any direction. In music/art/dance, the score generally has similar components: elements/themes/variations and ‘cues’ (or signals).
8. The initial tube-like structure of the score was inspired by the drawings of the embryo in Chapter 4.
9. These artworks were exhibited in ‘GAA: Holistic Science and Wisdom Tradition’, February–April 2019 at the Exchange, Cornwall.
10. Ideas for other images: How about a drawing that starts with one nucleus and evolves in many directions into many variations/potentialities of the process? And what about digression, regression and discontinuity? Could these traits be drawn into one image where we see a ‘healthy’ pathway and unhealthy or unsuccessful pathways simultaneously?

    Extending the scores through time: At the ‘top’ of each score, as the result of cell division, we get two nuclei. The image can continue to evolve through a forking/ramifying/fractal/rhizomatic structure.

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6

Drawing as Intuitive Mode for Representing Protein Dynamics

Gemma Anderson-Tempini, Jonathan 'J. J.' Phillips and John Dupré

Introduction

Any visual representation is an abstraction from the complexity of living process and necessitates the selection of some point of view. A core motivation for a process ontology is the observation that a pattern is actively maintained rather than given. Scientifically, we consider that living systems (on various scales of time and space) maintain unstable equilibria. The models we create and study of living processes and systems in the biosciences are dynamic and multi-dimensional, but the centrality of these features is not always sufficiently emphasized. One way in which these features can be brought to the centre of the researcher's or student's awareness, we propose, is by making the relation to the model more interactive. We are interested in drawing as a way of sustaining interaction between the researcher and the process they investigate from the lab all the way through to the model or the visual representation.

In this chapter, we – the project team of artist (Gemma), biologist (J. J.) and philosopher (John) – elaborate these suggestions by describing a series of experimental 'Drawing Labs' that that were held with the biologist's research group and addressed the problem of providing visual representations of protein folding and investigated how drawing techniques can be developed within a scientific research group to provide illuminating and informative representations of the dynamic and multi-dimensional processes that proteins go through. We also explored how these drawing techniques can be used as a means to interpret and theorize the processes they aim to represent. We are interested in drawing as an interdisciplinary and collaborative method for creating new images in line with new knowledge and in making visible unseen qualities of protein energy landscapes. Simple abstractions yield clear information, and more interaction, e.g. through protein topology diagrams which may be easily drawn by hand in a spontaneous manner, are conducive to dialogue and exploration. We seek such a mode to engage with protein folding and dynamics.

Proteins are a fundamental and highly diverse unit of organization common to all living organisms (the human genome encodes over 20,000 different proteins, some of which have hundreds of different so-called proteoforms). An overwhelming majority of biological processes at the molecular level depend on the function of protein molecules, and this fact is central to current efforts in biological and medical research. The creation, functioning and eventual secretion from the cell or recycling of a protein are spatiotemporally dynamic processes. Here we are interested in the problem of representing protein structural dynamics and their multi-dimensional character. We consider whether it is possible to display visually and interactively the key features of both the folding and functional trajectories of proteins and, at the same time, the energy landscape in which these trajectories take place.

The currently standard image for representing protein folding (thermo)dynamics in biology is the 'folding funnel'. This is a downward-pointing cone modified with additional geometric features to represent attributes of the energy landscape of protein folding. This model is well-established for good reason; it has features that represent some attributes well, such as the existence of multiple protein states and their relative stability. We found, however, that some features were not well represented, such as the journeys (trajectories) of individual proteins. We would argue that in its current state the 'folding funnel' image does not work well as an intuitive image or teaching aid, for example because the landscape fails to represent the undirected exploratory stochasticity of the trajectory taken or 'experienced' by an individual protein molecule. Folding funnels also do not give newcomers the opportunity to explore the folding process by manipulating a folding protein. There are also questions of how the development of protein structure relates to its potential energy[1] and how this is intrinsically connected to its environment (Fersht 1999). Perhaps the biggest obstacle to engagement with protein dynamics for scientists is the inability to relate it to something that is already known and well understood, and ideally something tangible that can be directly experienced. Hence, scientists rely on the conventional image of the folding funnel, which is similar to Waddington's 'epigenetic landscape', and other more relatable analogies, such as the golf putting green, ski slopes and so forth. Ultimately, a good deal of initiation is required in order to actively engage with this way of representing protein dynamics. We hope the images we produce in this interdisciplinary experiment and the process of their creation address some of these challenges.

Here, as is standard practice, we conceptualize the protein folding landscape as a surface upon which the protein system will travel. However, this already presents a significant conceptual challenge for beginners, as this is a surface with many dimensions (a manifold) – a high-dimensional space which is difficult to conceptualize and thus presents a barrier to dialogue, teaching and collaboration. The images we create through drawing are a flat representation (a projection) of that manifold. As observers in a three-dimensional world, we are most familiar with two-dimensional manifolds (e.g. an egg shell) and with three-dimensional manifolds (continuous solid objects; e.g. a ball of clay) (Riemann et al. 1892). In bioscience and mathematics (often the two go hand in hand), manifolds arise sometimes as physical entities in space (e.g. a cell membrane, perhaps described as a two-dimensional [2D] manifold like an egg shell), but often indirectly – as the parameterspace, or phasespace, for a biological entity or a geometric object in mathematics. Already our description faces the challenge of being a precise and accurate representation of theory yet conveying only an intuition of this somewhat complex concept. Therefore, it is common to create a more tangible 2D or 3D graphical representation, and the process of doing this with higher-dimensional objects is termed 'projection'. Visualizing such abstract descriptions through imagery in tangible 2D or 3D space can significantly help in understanding; most importantly, the significant attributes of a system can be given meaning with a far reduced degree of prior initiation, study and formalism – in this case, mathematical ability and physical theory. Nonetheless, it is not necessarily easy to recognize what is represented, as such simplifications and abstractions may allow multiple different interpretations.

The development of computerized simulations and techniques for real-time imaging at microscopic scales provides a partial solution to the problem of visualizing such *n*-dimensional entities, by providing, in effect, 4D projections of them. With these techniques, the scientist or any other viewer of the imagery is removed from the production of the representation, however, which negatively affects the quality of insight and inference. The production of such images requires great skill and knowledge, which are generally reserved for initiation. While the simplified images often used to represent a 2D energy landscape, such as a conventional protein folding funnel, are more amenable to the uninitiated practitioner, they do not provide access to many of the key features of the process to be represented and explored. The imagery thus relies on its ability to engage on an intuitive level and its clear representation of the formal underlying principles. Our central hypothesis in this collaboration was that an active drawing process may enable greater exploration and development of intuition without the significant overhead of formal training in protein folding, thermodynamics and kinetics.

The development of fast, automated imaging technologies has been a central factor in the recent decline of drawing practice in the life sciences

(Anderson 2014), a decline that has occurred despite the continued pervasive use of images in scientific practice and education. For educational purposes, images are now often ‘grabbed’ from the web or borrowed from a colleague, and although the teaching of science, technology, engineering and mathematics (STEM) relies heavily on visualizations, little attention is paid to the various representational and productive relations between these and the phenomena they purport to represent. Because the epistemic value of drawing in science is generally understood in terms of the drawing as an object and not, as is argued at various points in this volume, in the drawing process itself, the unique epistemological value of drawing has become increasingly under-appreciated (Anderson 2014; Tversky 2010; Wittmann 2011). Educationally, this has had costs in terms of student engagement, a deeper understanding of the conventions of scientific representations, and the development of ‘creative reasoning’ (Ainsworth et al. 2011). In general, the epistemic value to scientists of the activity of drawing has been overlooked (Anderson-Tempini 2014; Anderson-Tempini et al. 2015; Kozma et al. 2000). A unique advantage of drawing is its double nature as a tool for deepening understanding and for communication. Drawing helps to consolidate ideas, clarify concepts and bring visibility to thought. Drawing can extract and highlight salient information from what is discussed, observed and witnessed, and can be used to communicate and analyze an idea or a concept within a research team or to the broader public.

Representing process: Abstracting the protein

Gemma Anderson-Tempini together with molecular biologist Jonathan Phillips (J. J.) began a collaborative investigation into drawing protein dynamics. Each protein can be thought of as beginning its own ‘life cycle’ as the amino acid chain that emerges from a ribosome. Most such proteins ultimately adopt sets of defined ‘postures’ (‘native state ensembles’) in order to undertake physiological functions. The protein (considered in the first instance as a line) begins to explore 3D space as it emerges from the ribosome, even before it has reached full length. At this stage, the line will rapidly distort its geometry through a series of movements, which we describe with words such as stretch, vibrate, twist and fold, into the third spatial dimension to explore the ‘energy landscape’ (Figure 6.1). Some movements are strenuous (increasing Gibbs free energy – ΔG), some undirected (at a local-free energy minimum) and some transitional (at a local-free energy maximum). The dynamic protein chain finally comes to rest in a native state with relative stability at the global-free energy minimum. Whilst a single protein ultimately experiences a 4D (3D + time) protein folding

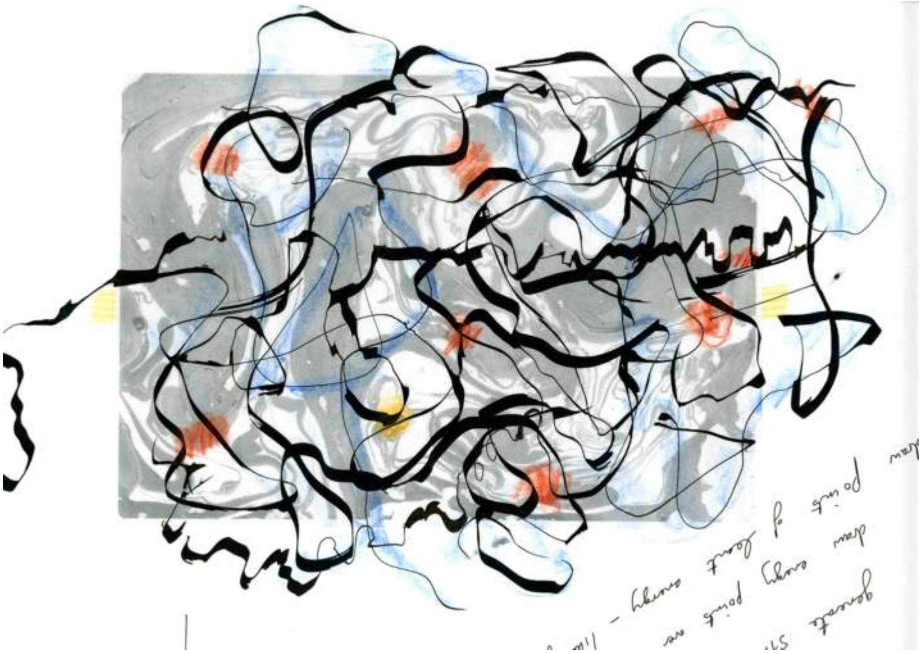


FIGURE 6.1: Gemma Anderson-Tempini, ‘Intrinsically disordered protein’. Ink on tracing paper on marbling paper, 2018.

journey and subsequent functional lifetime, the energy landscape in which we think of this journey taking place is vastly higher dimensional (we can begin to imagine this space as something like the ‘24 cell’[2]) (Figure 6.2), which relates geometry to potential energy.

The protein we chose for initial exploration was the immunoglobulin G1 (IgG1) antibody. Antibody structure has features that we termed ‘arms’ and ‘legs’ and thus lends itself to an analogy with the human form and movement (Figure 6.3). This greatly facilitated the interdisciplinary communication necessary to begin a joint exploration of protein folding and dynamics, upon which one of us embarked without a formal scientific background. As soon as we drew simplified protein structures of the antibody together, the human body–antibody analogy offered up many terms for structure (arm/leg/elbow, etc.) and movement (bend/rotate/stand/lie), and even a common-sense interpretation of free energy language (relaxation/stress). In the process of drawing, we came to see the formation process (protein folding) of our antibody as analogical to the progression of a yoga class. The outset of the process is characterized by restlessness and a high degree of agitation and random motion (representative of the intrinsic disorder of the denatured polypeptide). There follows a sequence of high and low-energy postures – often guided by a teacher (like a chaperone protein). In the end, a relaxed ‘native’ state

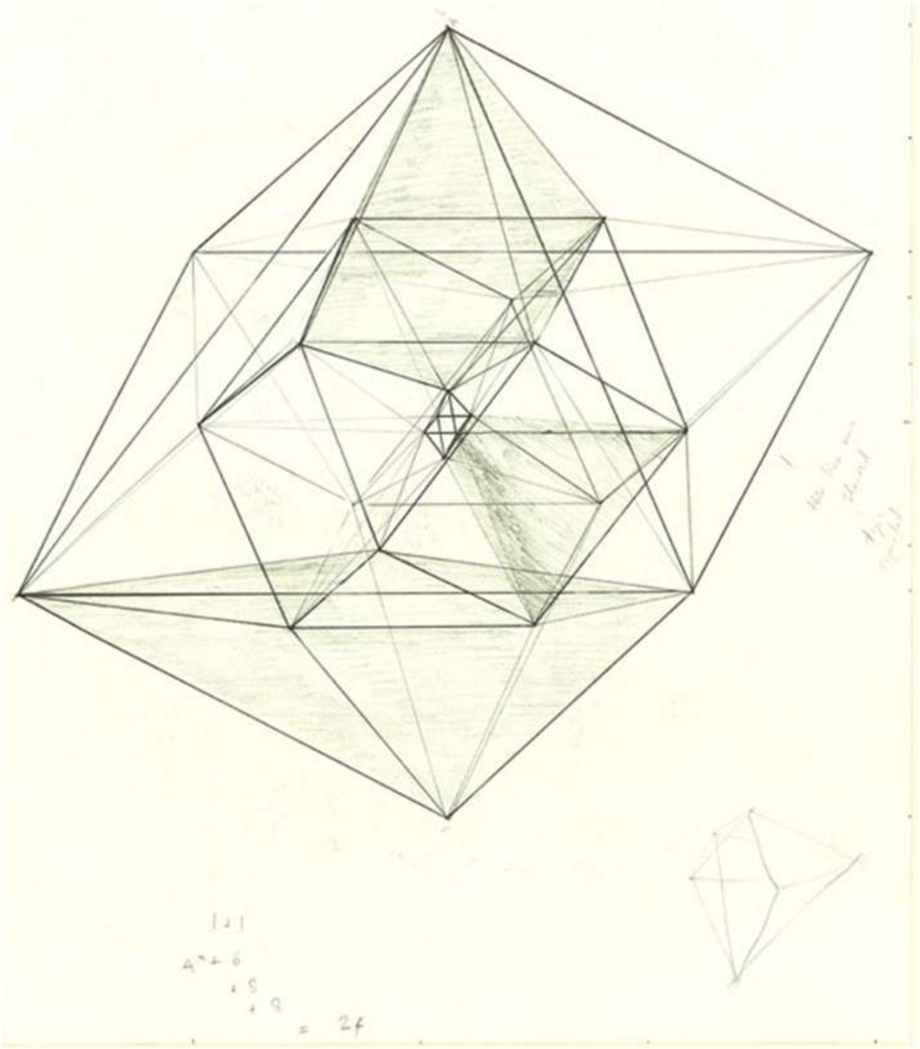


FIGURE 6.2: Gemma Anderson-Tempini and Alessio Corti, ‘The 24 cell tetrahedra’. Pencil on paper, 2018.

is reached. The constituent parts are unaltered (the human body remains intact, and the protein’s covalent bonds are not broken during folding), but the body has been relaxed in a manner that is difficult to achieve directly and spontaneously without undergoing this process.

Antibody movement sequences, drawn like a yoga flow, proved to be a simple way of capturing the pattern of postural change in protein folding (Figure 6.4). In these drawings, movement arises out of the relationship between postures in the series. These drawings gave us an entry point for discussing protein dynamics[3] and energy changes visually, and they demonstrate that it is possible to discover an alternative, intuitive way of knowing and representing microscopic phenomena, such as those involved in protein thermodynamics, including

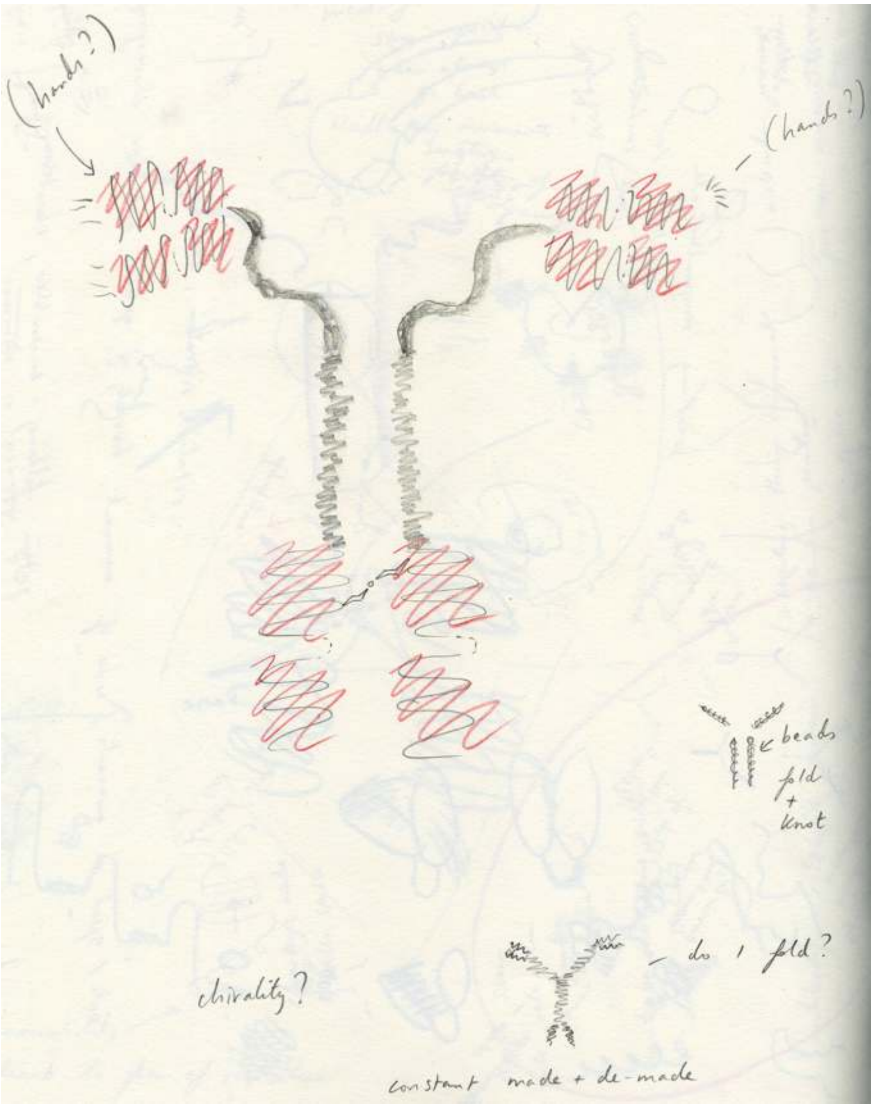
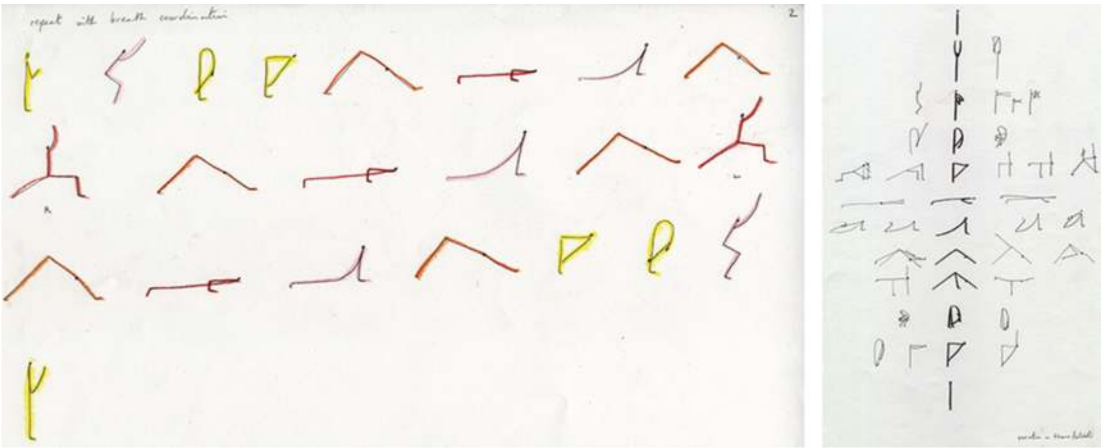


FIGURE 6.3: Gemma Anderson-Tempini, ‘Drawing of the IgG1 antibody structure’. Pencil and coloured pencil on paper, 2018.

chaperone-assisted folding to avoid local thermodynamic minima (which can be thought of as traps).

A process ontology treats a physical object as a more or less temporary structure, which is more or less effectively stabilized by its internal activities and its interactions with its wider environment. In the context of protein folding, the structure and energy landscape of the protein are co-constituted and there is no precise boundary between the protein and the surrounding activities with which it is engaged. Our next challenge was to find a way to represent both the protein and the energy landscape and to do so in a



(A) (B)

FIGURE 6.4A and B: Gemma Anderson-Tempini, 'Yoga flow drawings'. Pencil and coloured pencil on paper, 2018.

way that reflects the indeterminate/variable/permeable boundary between them.

The circular maze

After a few months, we had created a portfolio of exploratory drawings and notes. All of these were laid out on the floor of a large room for a meeting of the team, which included Gemma and J. J., philosopher of biology John Dupré, and the other members of J. J.'s lab. At this point, the problem of representing the protein energy landscape was still unresolved. In a discussion about the nature of the landscape, J. J. described the protein folding funnel model – often used in the field for teaching purposes – as an upside-down cone with a narrow point that corresponds to the native state of the protein. Gemma proposed that a maze might be an effective visual template if the centre of the maze coincided with the point of the cone (the 2D circular maze is an unfolded or flattened 3D cone). During the meeting, Gemma experimented with paper models of the maze she had constructed (Figure 6.5); she drew a 2D circular maze to be cut and folded to create a 3D maze cone. She realized that the 2D circular maze also had advantages as a metaphor. For example, the embodied process of drawing the path/trajectory through the maze structure is comparable to protein finding its way through the energy landscape.[4]

We discussed the nature and composition of mazes (dynamic mazes, fluidity, interconnection, layering, maze vs. labyrinth, etc.) and explored how their features might serve as metaphors for aspects of protein folding. For example,

FIGURE 6.5: Gemma Anderson-Tempini, photograph of ‘Paper maze/cone models’. Paper, 2018.

the branching and joining of paths in a maze may depict the alternative trajectories of a protein travelling through a folding landscape, capturing features such as stochasticity and the thermodynamic equivalence of microstates. The imagined movement of a protein through the maze is also in many respects similar to movement through an epigenetic landscape as described by Waddington (see also Anderson-Tempini et al. 2020). John advanced the suggestion that the maze could work as a metaphor for biological processes across multiple scales.

The team agreed to explore the maze idea. Gemma began to experiment with different ways of drawing a maze (Figure 6.6) and together with J. J.

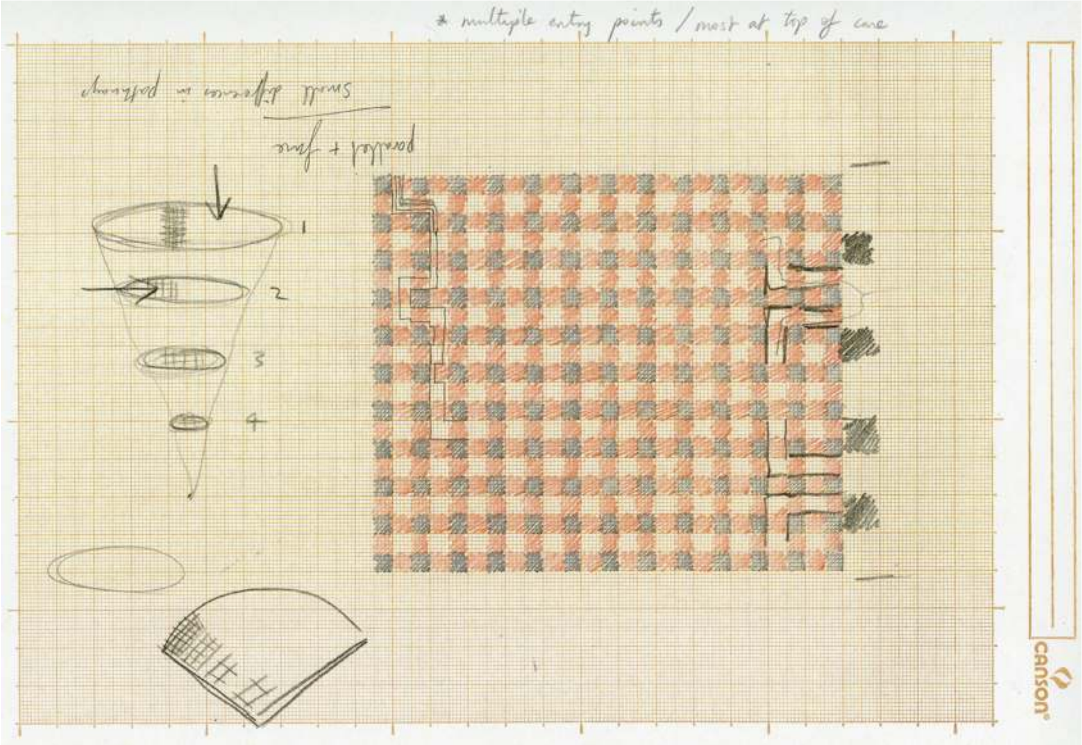


FIGURE 6.6: Gemma Anderson-Tempini, ‘Initial experiments with drawing a maze’. Pencil and coloured pencil on paper, 2018.

devised ways of adjusting the drawing of the maze to depict features of the protein folding landscape. One feature of the maze that proved very useful was granularity, i.e. the size of the grid (Figure 6.7). Granularity could be used to define the proximity of available changes in direction, which could be used to represent features of the protein’s environment such as the steepness of the energy landscape. The maze now provided us with a metaphor for the protein folding landscape as well as an interactive drawing method to visually create variations of structures and features of the landscape. Drawing the dynamic nature of the protein in the maze enabled us to go beyond illustration and standard representations and to enact and mimic features of the protein.

Geography of the maze

The circular maze is comprised of three areas of different potential energy available to the protein. On the outside, which represents the protein entering the folding

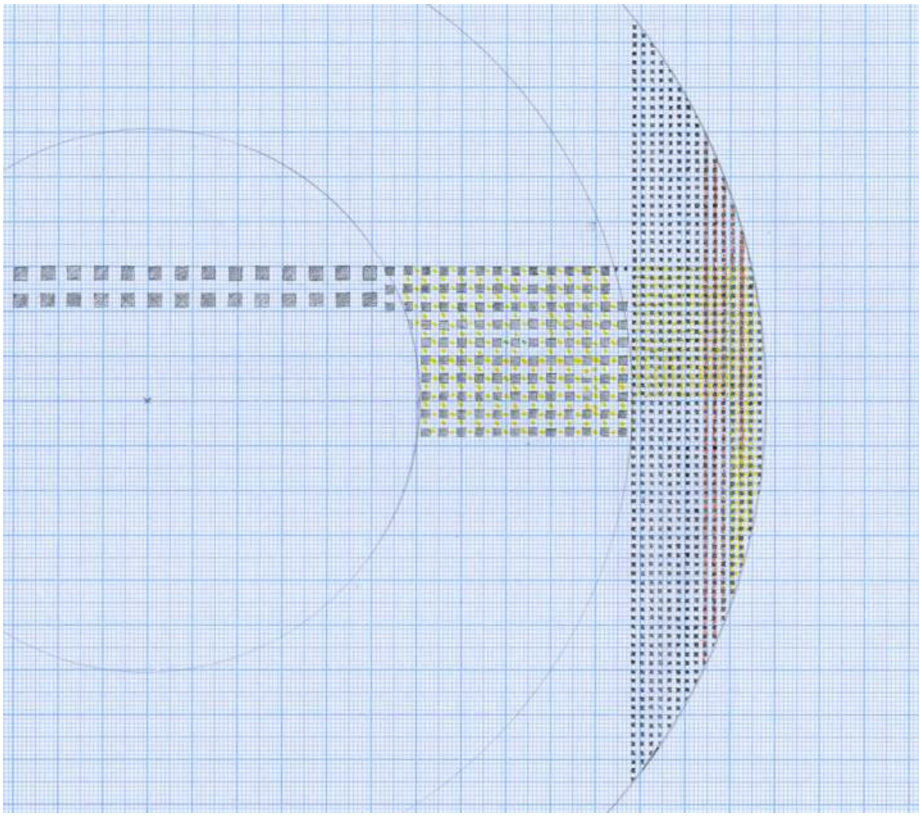


FIGURE 6.7: Gemma Anderson-Tempini, 'Initial experiments with drawing granularity in the maze'. Pencil and coloured pencil on graph paper, 2018.

landscape, the potential energy is high; in the central area of intermediate potential energy, the protein explores possible pathways; and eventually, the protein reaches the area of low potential energy in the centre (Figure 6.8), i.e. the native state.

The outer ring has a texture that is relatively fine-grained. This allows us to emulate features of a protein folding landscape such as the existence of multiple entry points, a steep descent, fusion and branching. The middle ring has intermediate granularity and interfaces with the inner and outer rings. This represents features of a partially folded immature protein, such as exploration and meandering through turns, uphill or backward travel. There are also fewer entry points from the outer ring into the middle ring than into the outer ring itself. The structure of the inner circle is coarse-grained (sparse), and there is a single interface that connects to the middle ring. This emulates the final stages of the protein folding process, in particular the reaching of a global energy minimum (i.e. the termination of the maze) and protein folding landscape roughness, and offers an intuitive representation of the reduction in choice and entry points compared to the higher energy levels (i.e. outer rings).[5] The granularity

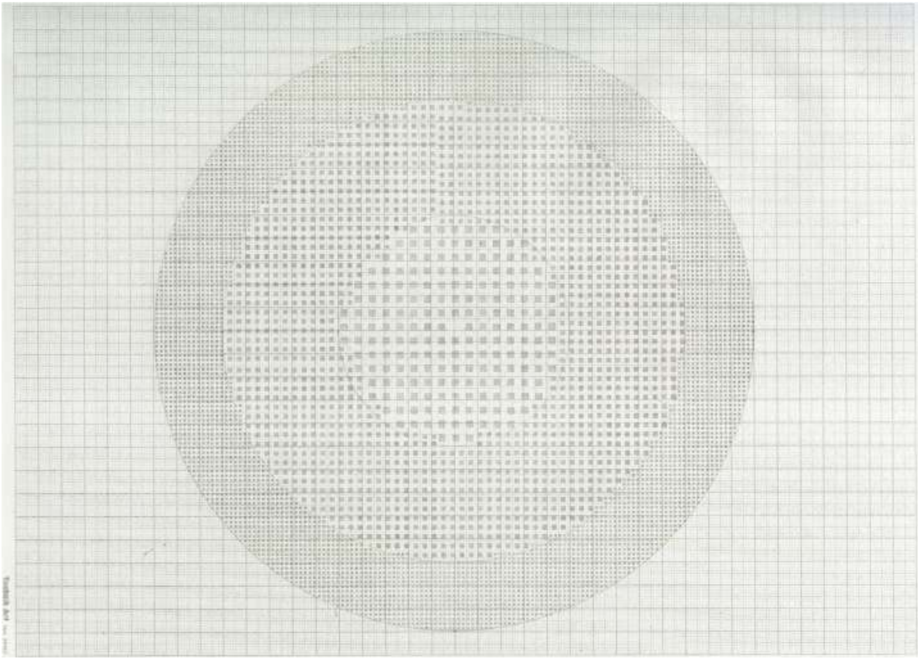


FIGURE 6.8: Gemma Anderson-Tempini, 'Circular Maze'. Pencil on paper, 2018.

and other features (e.g. colour) represent many of the important features of the landscape: relative stability/instability (centre of maze: stable; outside of maze: unstable), stochasticity (backward and off-pathway randomized turns), nonlinearity (zig-zag trajectory), vibrational energy and entropy (line as a scribble with high or low frequency), potential energy (e.g. colour gradation), postural and morphological change and so forth. These features can be adjusted to represent a wide variety of protein dynamics.

The structure of the maze can be used to represent the countless possible folding paths and multiple 'solutions' to the maze. Apart from the 'ideal' path, there are likely to be several other ways of reaching the point of lowest energy. Although there may be a single grouping of paths that are thermodynamically or kinetically equivalent, there may not be a single optimal route. This also points to the general usefulness of the maze image, as multiply accessible attractor states are a feature of many biological processes.

Moreover, through the drawing process, the image becomes interactive. The drawing is informed by the Phillips lab members' knowledge of the protein and created by enlivening this knowledge and visually imagining the dynamic nature of the protein. The grid is like a game, and the drawer is the player. There are many ways to play the game, and many ways to *be like* the protein; the maze drawings allow for an imaginative mimicry of the protein as energy landscape. This imaginative process is

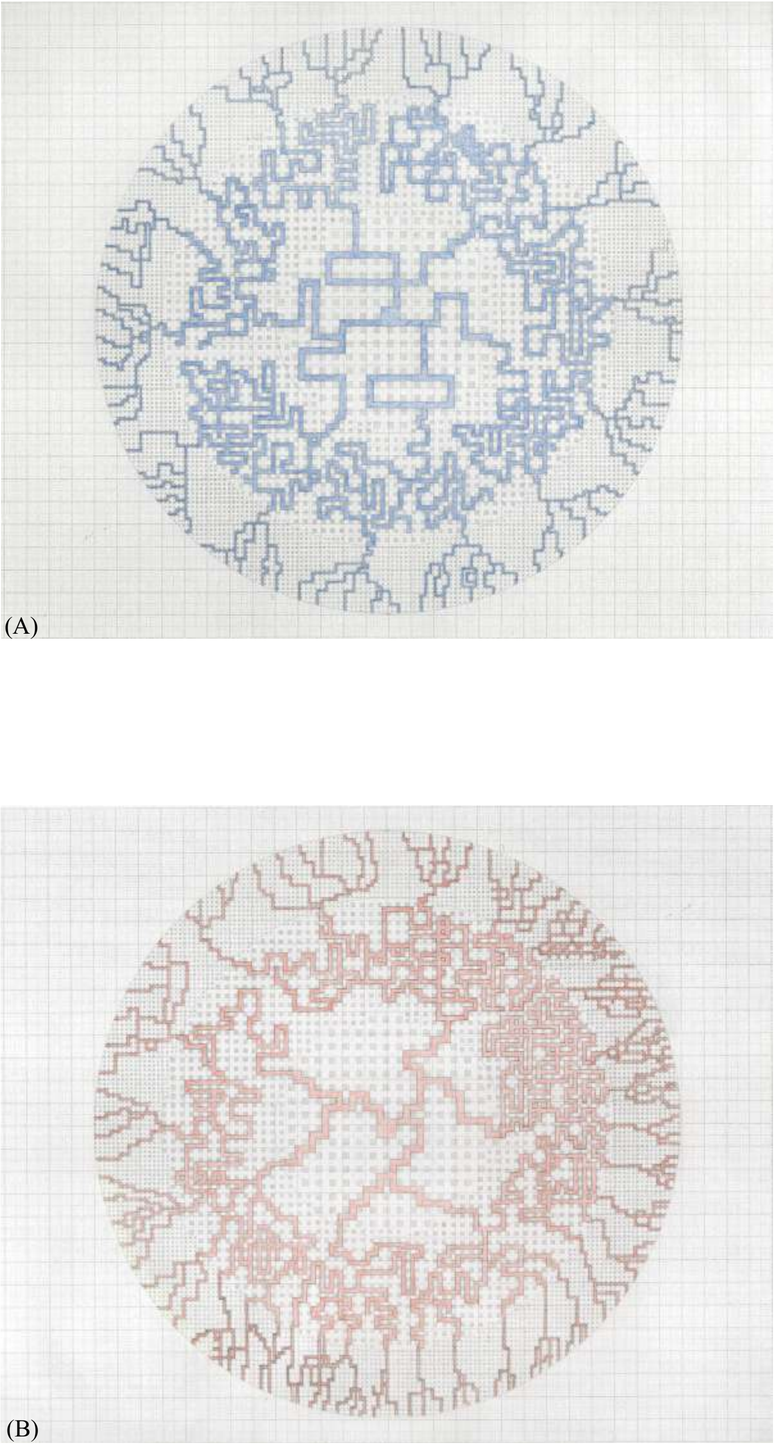


FIGURE 6.9A–C: Continued

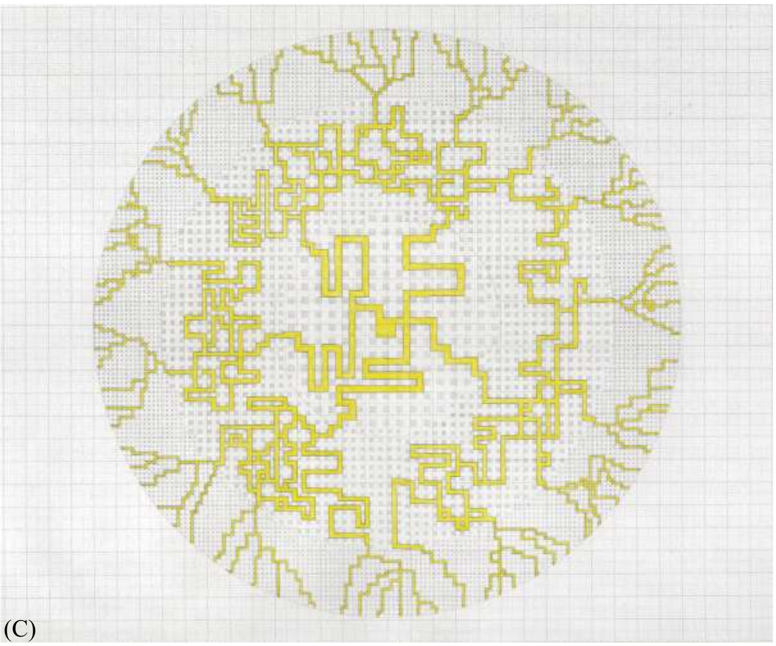


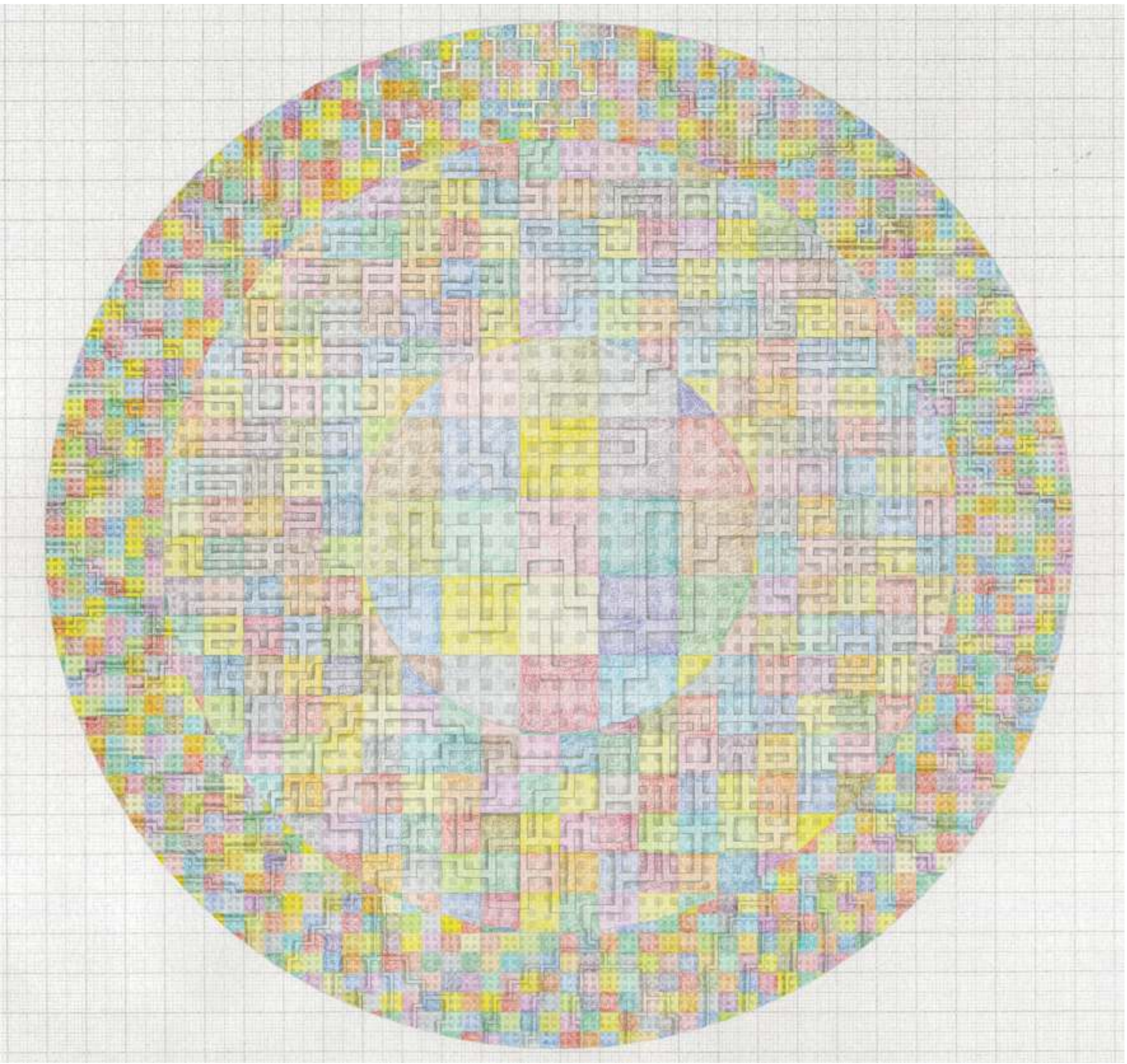
FIGURE 6.9A–C: Gemma Anderson-Tempini, 'Protein maze/garden of forking paths'. Pencil and coloured pencil on paper, 2019.

enhanced by the ability of the maze to incorporate features that represent attributes of the protein and its folding pathway(s) that are not captured by conventional energy landscapes. Drawing within the maze template facilitates interaction, as opposed to passive engagement with a pre-prepared image.

Testing the maze: Collaborative drawing of the haemoglobin protein

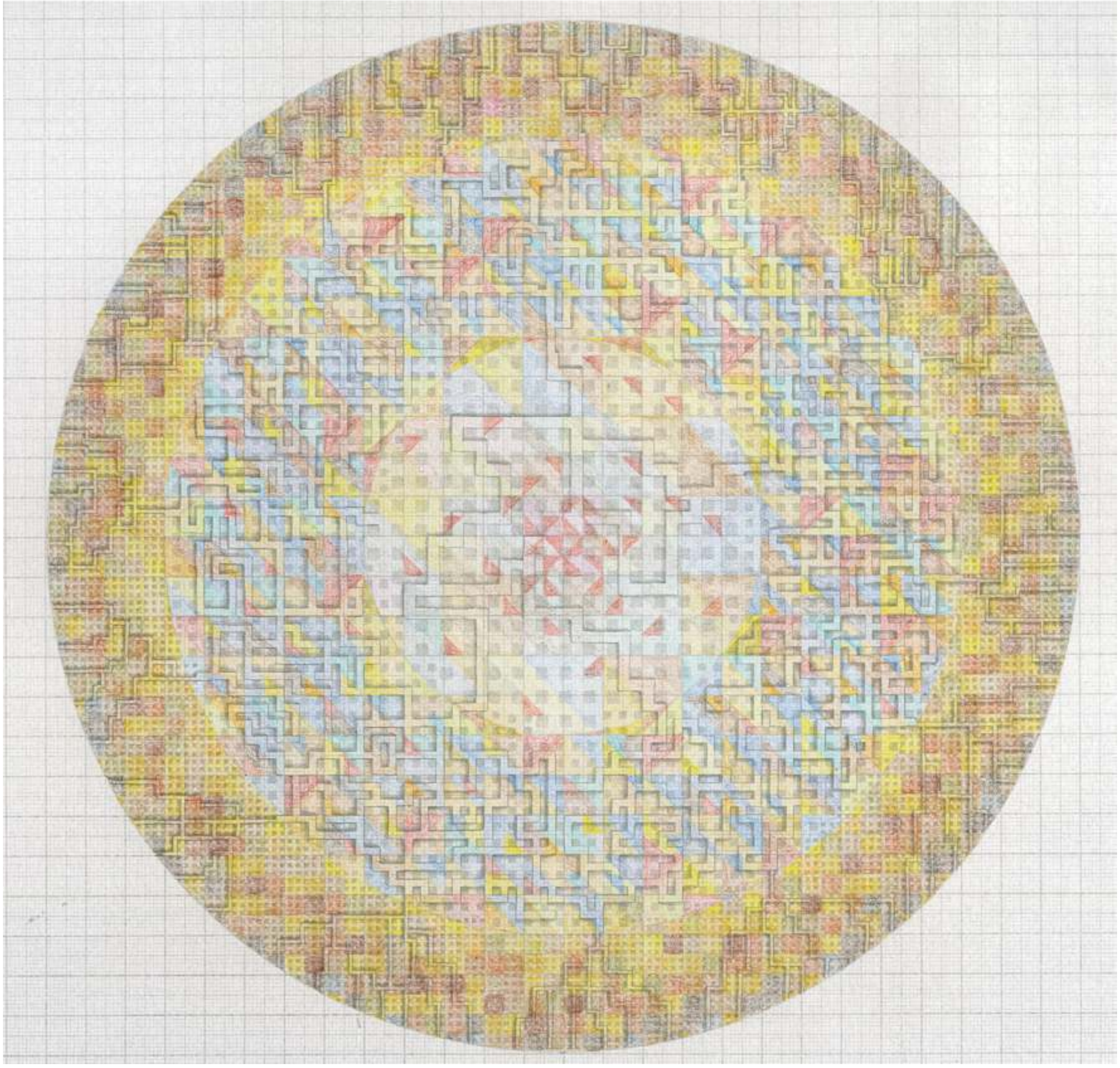
All of this raised the exciting possibility that the change in the presentation of an energy landscape from a folding funnel to a maze may enhance relatability (via a shared human–protein perspective) and thus energize the exploration of individual protein trajectories.

Thus, to test the potential of the maze to serve as a catalyst for drawing and developing concepts of the protein landscape, we asked the members of the Phillips lab to participate in a series of nine two-hour Drawing Lab sessions in 2019. All participants agreed to use the maze structure as a basis for experimentation and to address the general theme of protein folding. Each Drawing Lab began with Gemma presenting a set of ideas, themes, questions and images. Several participants were wholly uninitiated in the theory of protein thermodynamics, folding and dynamics, and a further key objective was to develop an intuitive understanding of



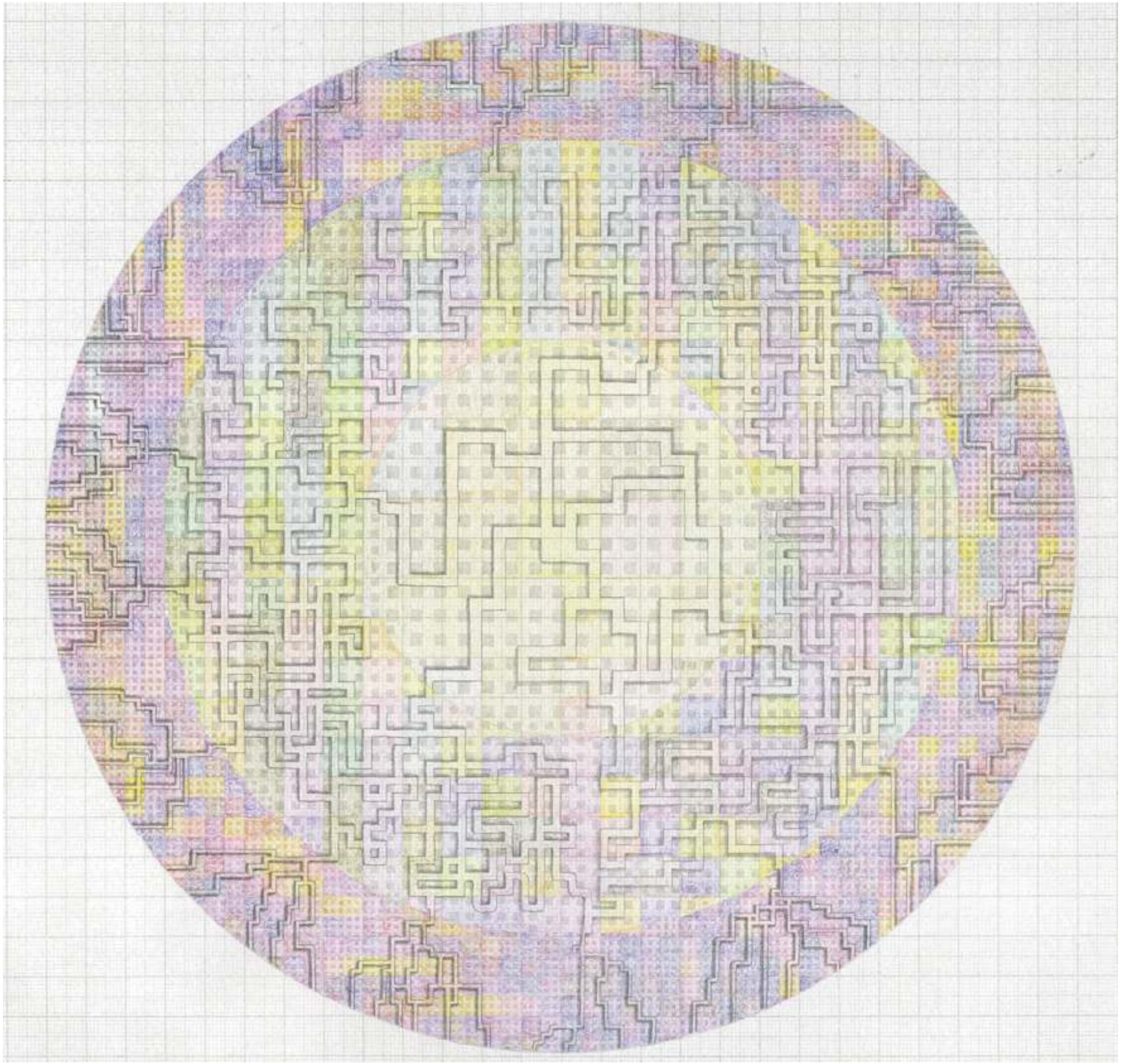
(A)

FIGURE 6.10A–C: Gemma Anderson-Tempini, ‘Protein maze/garden of forking paths’. Pencil and coloured pencil on paper, 2019.



(B)

FIGURE 6.10A–C: Gemma Anderson-Tempini, ‘Protein maze/garden of forking paths’. Pencil and coloured pencil on paper, 2019.



(C)

FIGURE 6.10A–C: Gemma Anderson-Tempini, ‘Protein maze/garden of forking paths’. Pencil and coloured pencil on paper, 2019.

this process through collaborative drawing. However, participants found engagement in the creative process of the Drawing Lab as important as any other scientific output, and this mindset resulted in questions, insights and the rapid development of a common language.

Here we focus mainly on how the group developed drawings of haemoglobin – a protein more or less familiar to all bio-scientists and much of the wider scientific community. Because the structure of haemoglobin changes each time the protein binds and releases oxygen, it is often referred to as the 'breathing molecule'. The group began to draw on one of the maze templates, first the process of haemoglobin becoming oxygenated (in the lungs) and then the release of oxygen (in muscle). Different colours were used for different phases of this process; red for oxygenation and blue for deoxygenation. As we drew, we discussed how this process is continuous and repetitive (with a modicum of variation on each iteration), and we experimented with drawing visual forms such as a sphere, a figure of eight and connected cones to represent what we had drawn in the circular maze. To test these ideas, Gemma made photocopies of the drawings and cut them to create cones, which we physically connected in a way that alluded to the continuous breathing of the molecule (Figure 6.11). We imagined many of these cones connecting like a series of hourglass forms, each iteration comprising repetition and variation. We read this model as a map of oxygenation and deoxygenation, but more generally as a representation of stability and instability, high and low energy and of activity.

Haemoglobin consists of four protein subunits, each of which is very similar to the myoglobin protein. So for simplicity, at this point, we switched to working on myoglobin, which is only one-quarter of the size of haemoglobin (and binds either one oxygen molecule or none at all) and therefore provided a more manageable model for exploring complex concepts such as protein functional switching.[6] Again, the group began to collaboratively draw on the maze template Gemma had prepared, taking inspiration from images by artists Vasarely and Klee (Figure 6.12). In this session, the focus was on deforming and de-centring the maze through drawing and experimenting with mosaics of codified shapes (Figure 6.13) that represent energy maxima and minima, pathway blockades and molecular degradation. At the same time, Gemma and J. J. shared the drawings they had jointly made of haemoglobin and of myoglobin (Figure 6.14), and the group used these drawings to integrate aspects of the maze and the mosaic (Figure 6.15). The resulting drawings represent protein folding, protein function and the protein life cycle through reshaping both the landscape and the pathway; as the landscape changes, so does the pathway, and vice versa. This initial exploration raised questions about how to draw the life-span of the protein so as to include processes such as protein recycling.

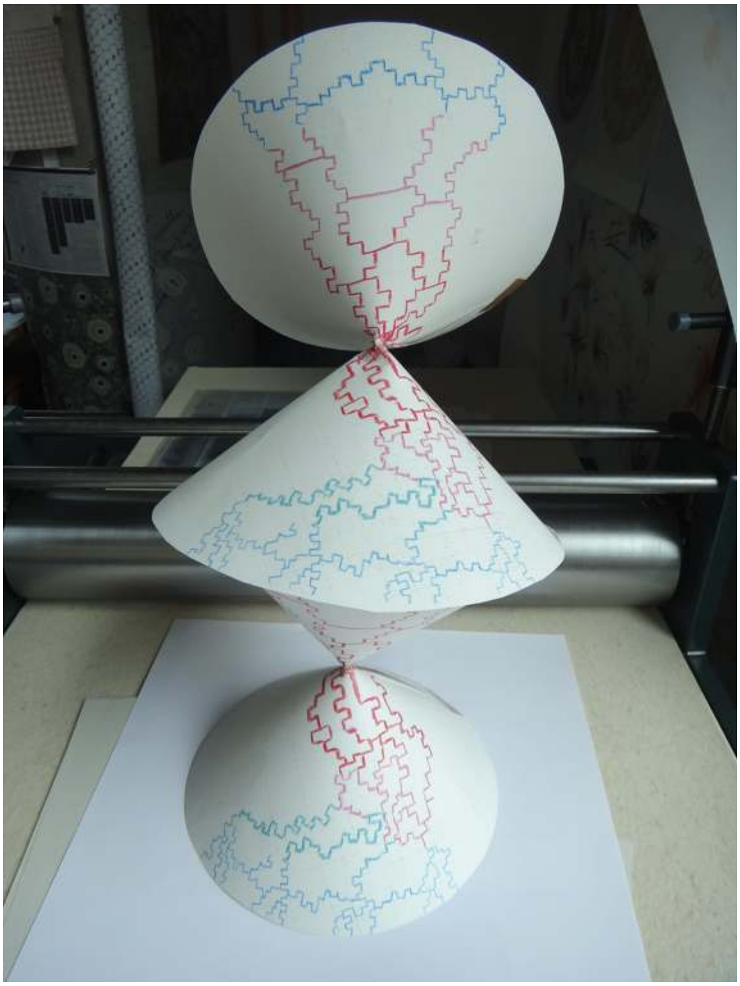
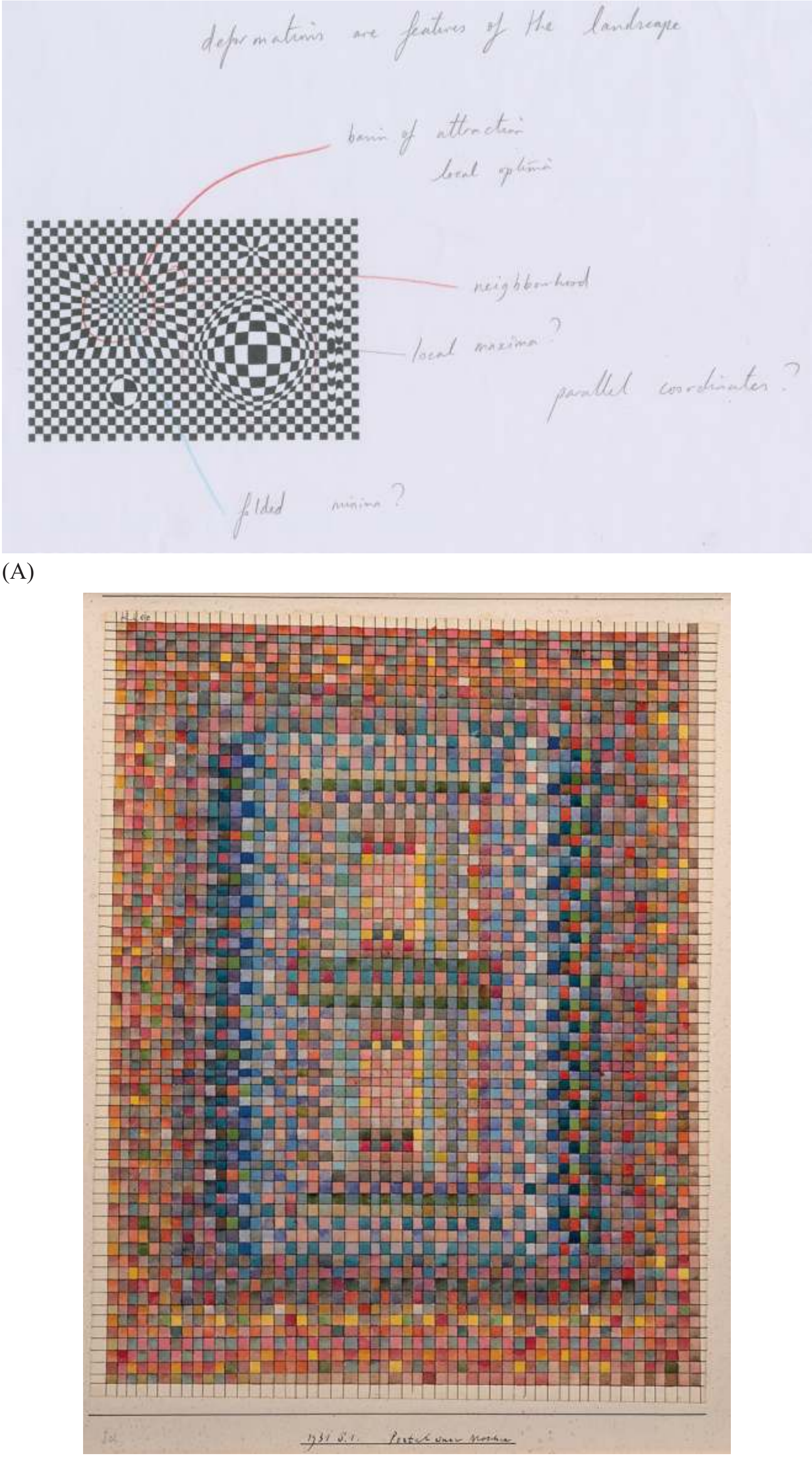


FIGURE 6.11: Gemma Anderson-Tempini, photograph of ‘The breathing molecule’. Pencil and coloured pencil on folded paper.

As we continued to refine the landscapes of myoglobin and haemoglobin, Gemma adapted two new maze templates, one which inverted the granularity of the grid on the maze for further drawing experiments (Figure 6.16) and one with a ‘collage’ maze landscape based on the previous drawing session (Figure 6.17). We drew and discussed the four units of haemoglobin (monomers), their neighbourhoods[7] in the map (representative of stable states at thermodynamic equilibrium), and pathways towards the oxygenated (‘bound’) state[8] at the centre. Importantly, the individual units of the protein do not always reach the centre, which sparked a discussion about protein misfolding. One participant proposed that a spiral template form might help to visualize this convergent dynamic process and later circulated an e-mail[9] with a drawing (Figure 6.18). This inspired Gemma to create a new template (Figure 6.19), and this new spiral template became the



(A)

(B)

FIGURE 6.12A and B: (A) Victor Vasarely 'Vega' (with annotations), 1957. Acrylic on canvas, 195 × 130 cm. (B) Paul Klee, *Portal of a mosque,* 1931.

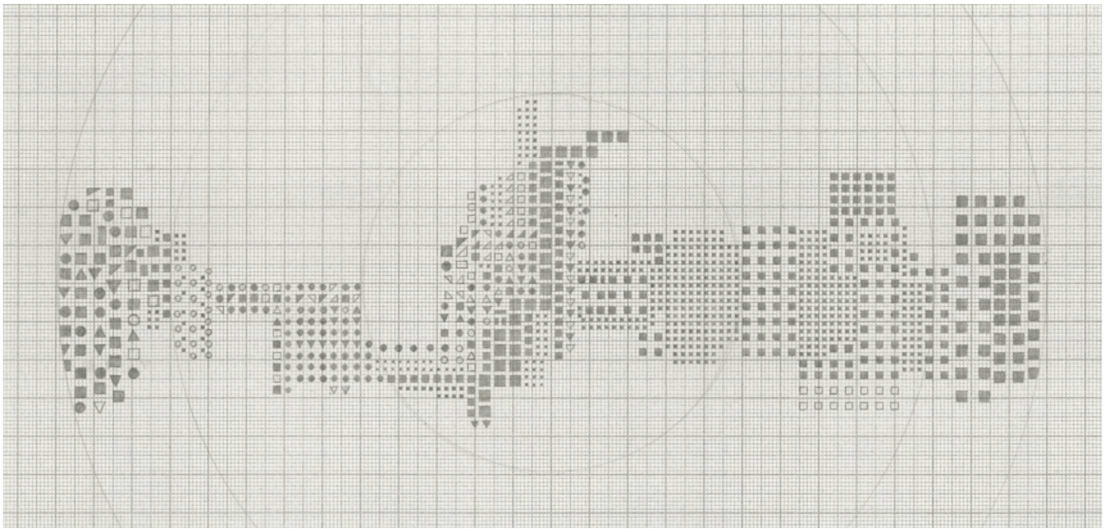


FIGURE 6.13: Gemma Anderson-Tempini, ‘Experiments with mosaics/codified shapes’. Pencil on paper, 2018.

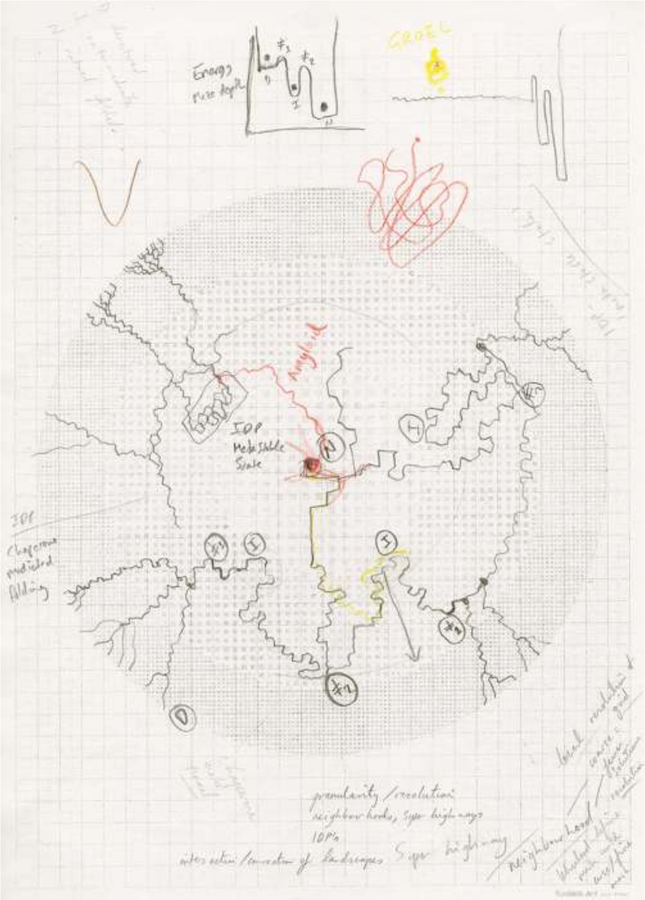


FIGURE 6.14: Gemma Anderson-Tempini and Jonathan Phillips, ‘Drawings of haemoglobin and myoglobin processes’. Pencil and coloured pencil on paper, 2018.

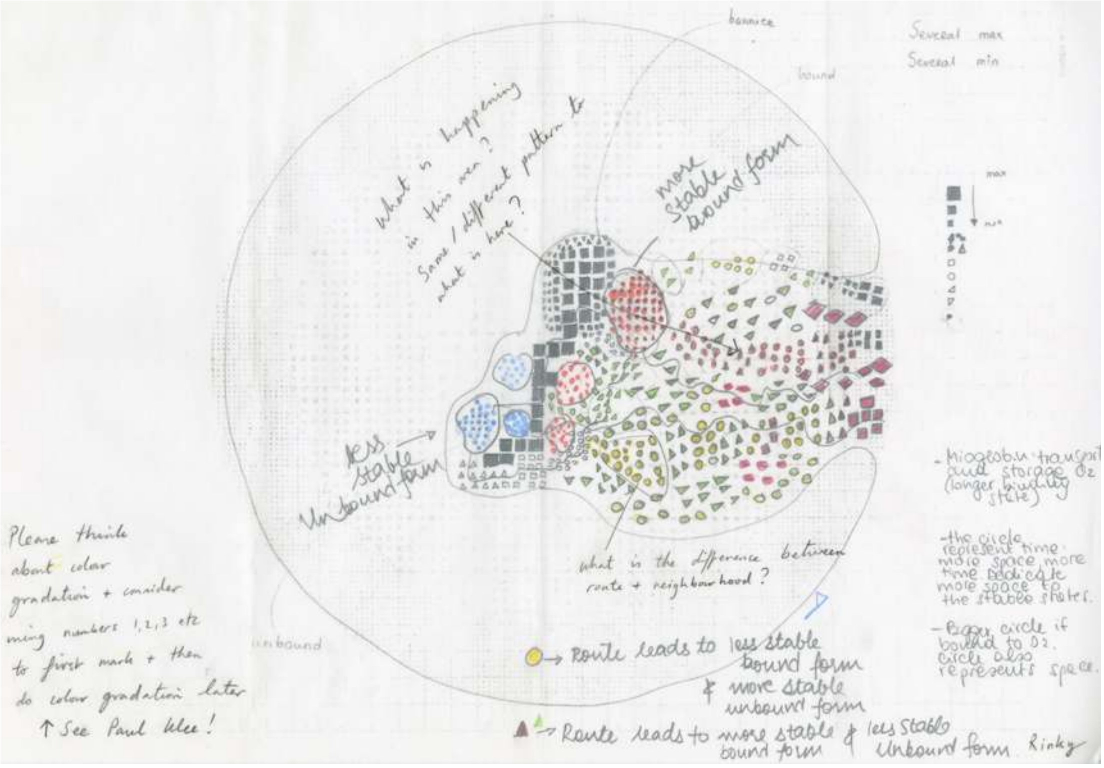
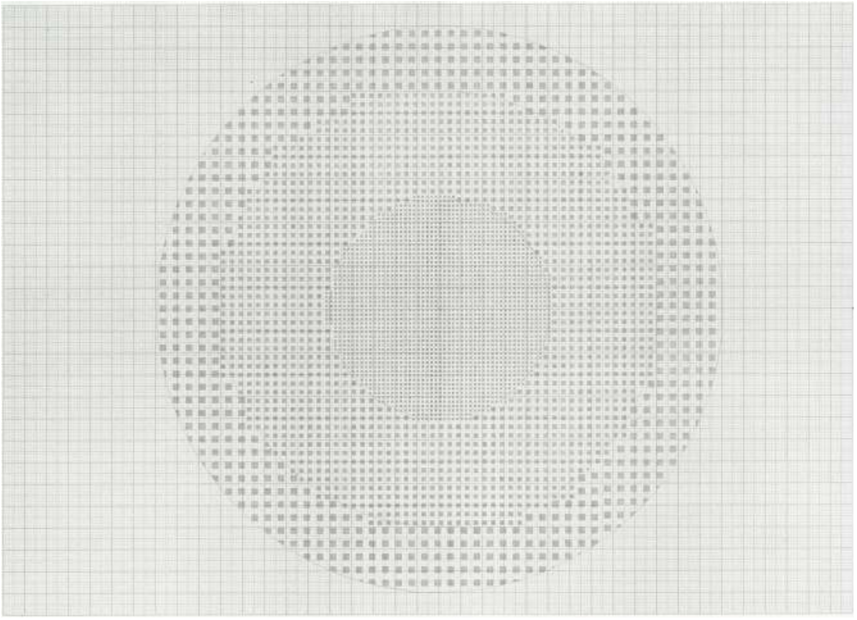


FIGURE 6.15: Drawing Lab participants, ‘Integrating aspects of the maze and the mosaic’. Pencil and coloured pencil on paper, 2019.

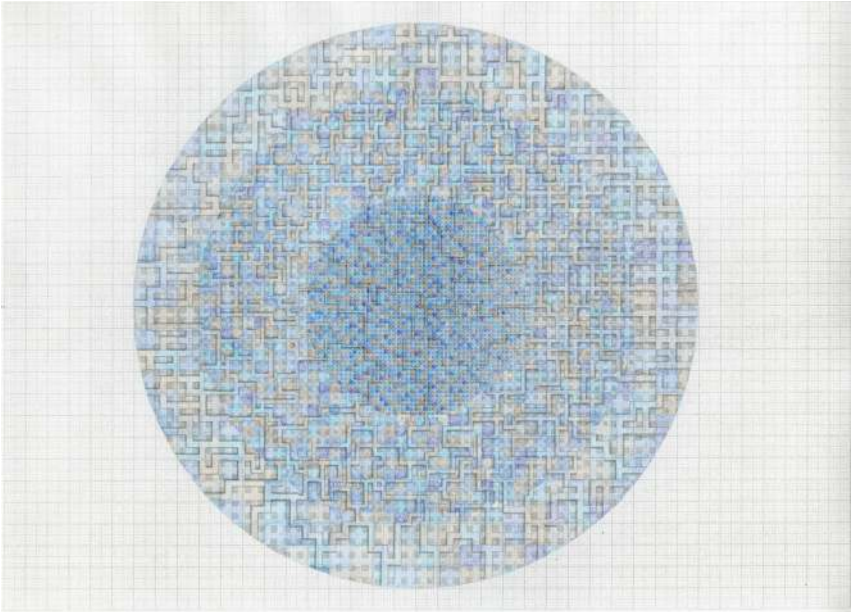
basis for further, more tightly guided, exploration of bound and unbound states of haemoglobin.

To conclude this section, we present the following categories of dynamic processes that we have attempted to represent with the help of the maze:

Towards representing co-operativity: As our collaborative process developed, a number of questions and reflections arose.[10] First, whereas a circular maze typically has one centre, many proteins – and the functional processes they undergo – rely on more than one stable state, and so their maze landscapes possess more than one centre. The maze for haemoglobin (de)oxygenation has five centres; in other words, there are five stable, functionally distinct states with zero, one, two, three or four oxygen molecules bound to the protein. The probabilities of transitions between these states differ due to co-operativity between different subunits of the protein. So, how might such co-operativity be represented in the maze drawing process? We had some success with what we termed ‘multi-basin landscapes’ (i.e. maze landscapes with more than one centre), and it would interesting to consider



(A)



(B)

FIGURE 6.16A and B: (A) Gemma Anderson-Tempini, 'Maze template with inverted granularity'. Pencil and coloured pencil on paper, 2019. (B) Gemma Anderson-Tempini, 'Inverted protein maze'. Pencil and coloured pencil on paper, 2019.

to what extent this maze model can be developed to gain an intuitive understanding of protein folding and dynamics as the protein interconverts between these various stable states.

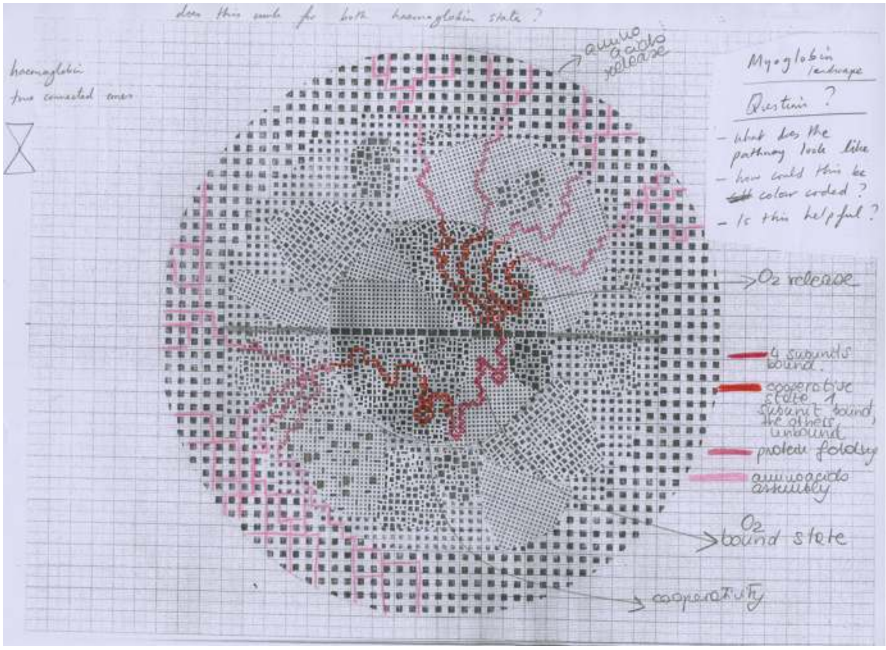
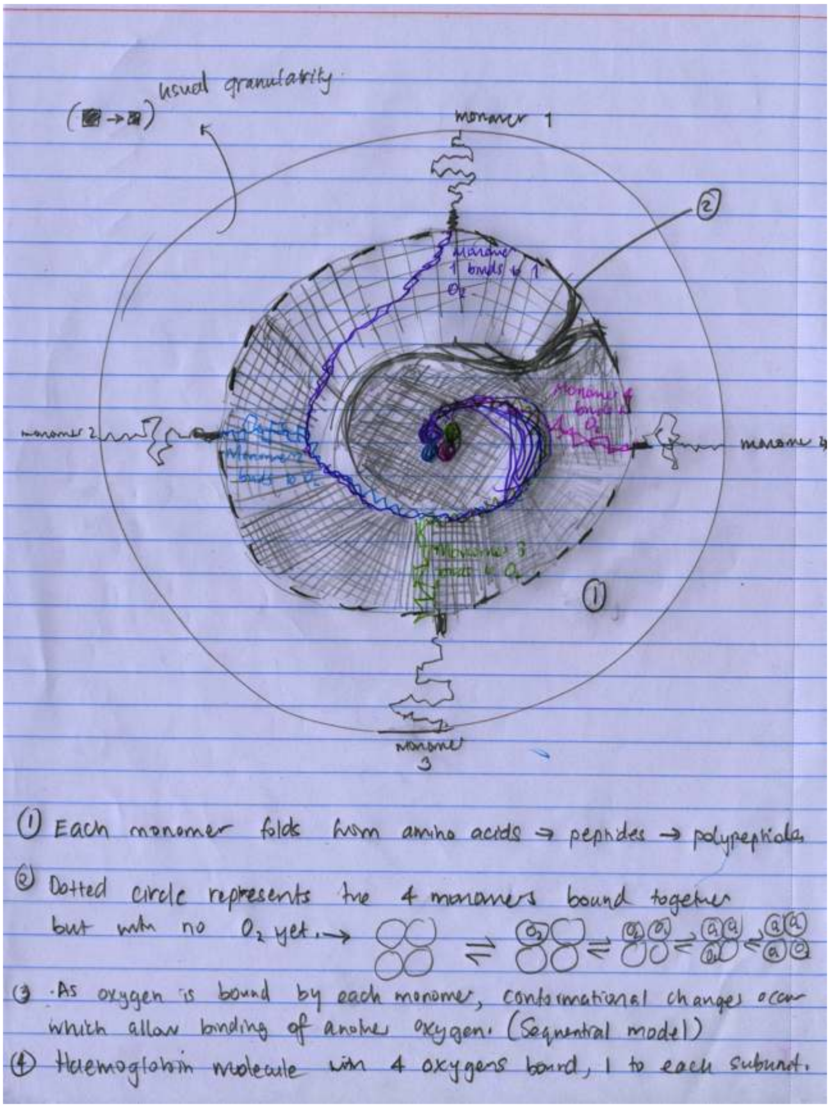


FIGURE 6.17: Gemma Anderson-Tempini, ‘Collage maze template’ (with annotations). Pencil on paper and collage with photocopies, 2019.

Towards representing topography: As already mentioned, our model of protein folding has many starting points, but one central destination in the maze. Participants naturally drew lines that explored the stochasticity as they tried to reach the centre; nobody simply drew a straight line, and everyone varied the trajectory and explored the landscape in a pseudo-random manner. The participants’ ‘curious hands’ (Myers) explored the micro-‘gestures’ of the protein and conveyed their understanding of molecular movements to themselves and to each other. During the tactile process of drawing, we also explored ways of physically deforming the circular maze drawings. We imagined pulling the grid upwards or downwards, like a fishing net, to deform the grid structure. The corollaries of this were discussed, for example, adjacent deformations could facilitate the creation of eddy currents in the fluid pathways of a protein. A, hitherto unexplored, possibility would be to use a deformable material (e.g. fabric) to print the maze pattern in order to represent maxima and minima in 3D.

Towards representing multiple stable states: We also began to develop a spiral landscape template (Figure 6.20) for representing the multiple – bound and unbound – states of haemoglobin and experimented with a new haemoglobin maze structure that maps areas of stability and instability for each of the four subunits of the



① Each monomer folds from amino acids → peptides → polypeptides

② Dotted circle represents the 4 monomers bound together but with no O_2 yet. →

③ As oxygen is bound by each monomer, conformational changes occur which allow binding of another oxygen. (Sequential model)

④ Haemoglobin molecule with 4 oxygens bound, 1 to each subunit.

FIGURE 6.18: Drawing Lab participant, ‘Spiral pathway’. Pencil and coloured pencil on paper, 2019.

protein. Working together on this template allowed us to develop the spiral model concept practically. The spiral image well represents the concept of a bidirectional sequential process (i.e. A↔B ↔C ↔D ↔E) but we are still unsure how to represent the interfaces (energy barriers) between neighbourhoods (equilibrium stable states).

Towards representing folding and binding: Experiments with the spiral pathway through the maze landscape also produced drawings in which the pathway changes colour (Figure 6.21) as oxygen binding happens, representing the crowding together of the four subunit components (monomers) in

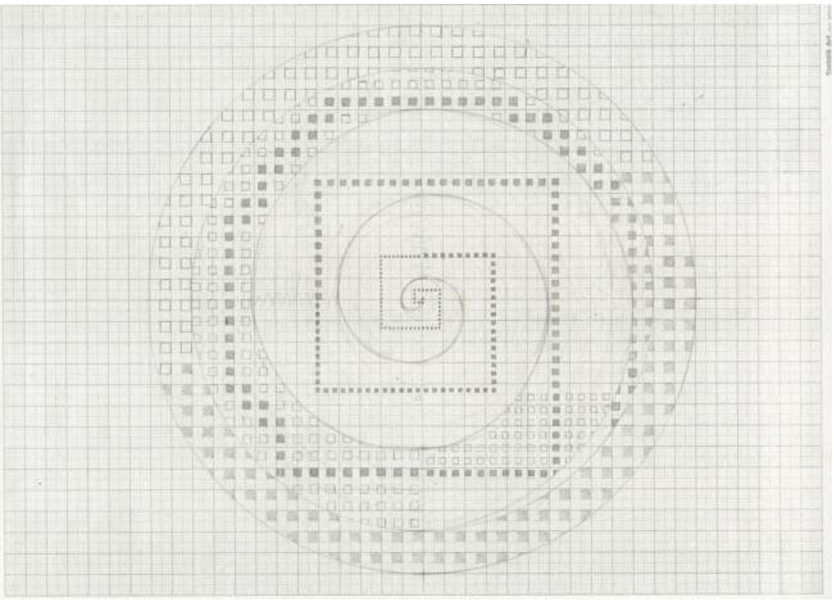


FIGURE 6.19: Gemma Anderson-Tempini, ‘Spiral template’ (in progress). Pencil on paper and collage, 2019.

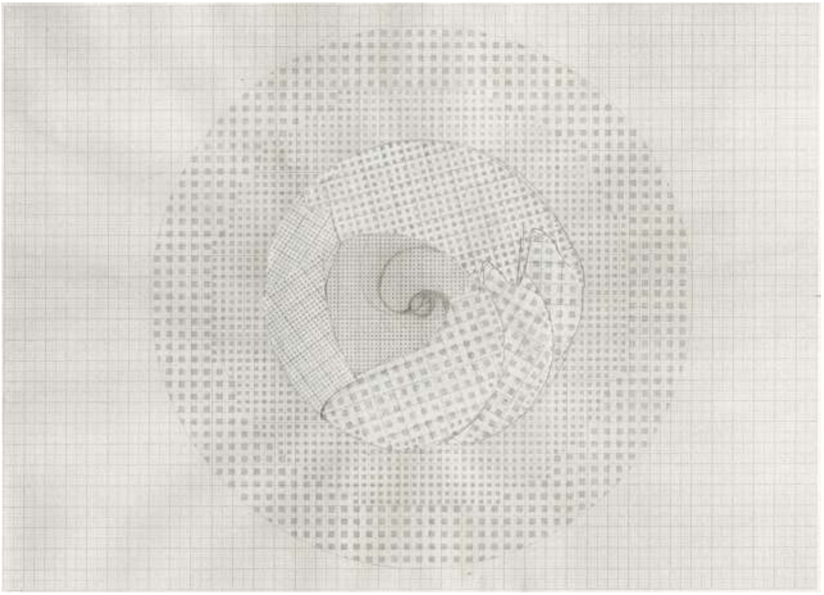
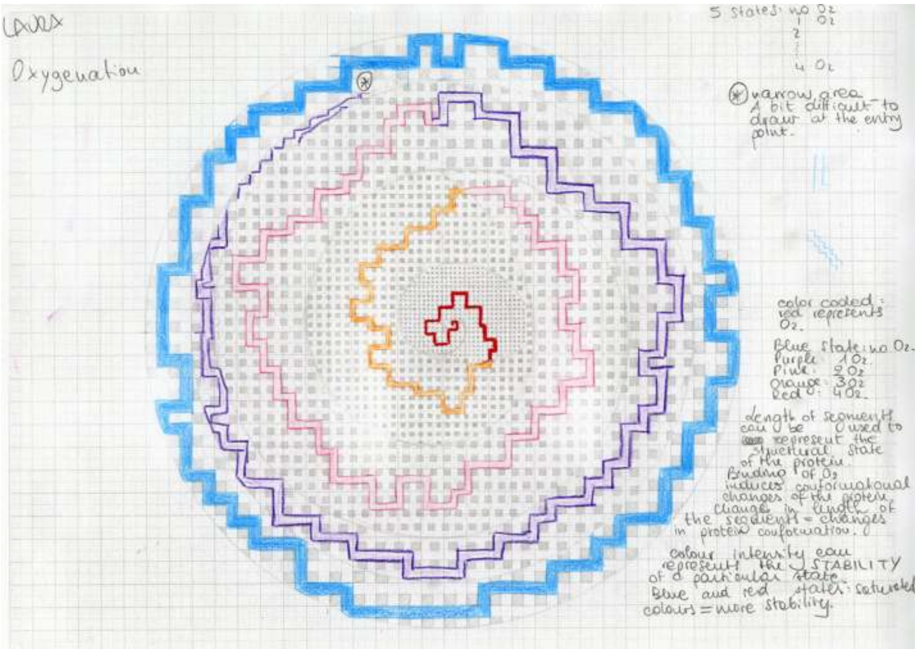


FIGURE 6.20: Gemma Anderson-Tempini, ‘Spiral landscape template for representing the multiple – bound and unbound – states of haemoglobin’. Colour pencil and pencil on paper, 2019.

haemoglobin, and the thickness of the blue line represents how many oxygen molecules are bound to the protein. In other drawing experiments, we explored wiggly vs. straight lines in a landscape, we developed ways of representing protein



(*) narrow area
A bit difficult to draw at the entry point.

color coded:
red represents O2.

Blue state: no O2.
Purple: 1 O2.
Pink: 2 O2
Orange: 3 O2
Red: 4 O2.

length of segments can be used to represent the structural state of the protein.
Binding of O2 induces conformational changes of the protein.
change in length of the segments = changes in protein conformation.

colour intensity can represent the STABILITY of a particular state.
Blue and red states: saturated colours = more stability.

FIGURE 6.21: Drawing Lab participant, ‘Spiral template with colour pathway’. Colour pencil and pencil on paper, 2019.

folding and oxygen binding in one and the same image: by placing the spiral maze inside a maze landscape designed for protein folding, which results in a big circle with many neighbourhoods/inner rings. The advantage of this is that the processes of folding and binding can be created simultaneously or sequentially, and the disadvantage is that it takes a long time to make such an image and requires many scales of granularity. Another promising avenue was to draw the folding and binding landscapes superimposed onto one another. In conclusion, this exploration of protein dynamics and how to represent them with a maze was engaging for all involved, and the exploratory process itself went some way towards generating the insight that a mature maze-based model might be able to provide.

Towards representing functional switching: We established that the landscapes for oxygenation and deoxygenation are different; they are more or less inverted.[11] Based on this realization, Gemma made two new grids where the spiral pathway is completed as the paper folds into a 3D cone (Figure 6.22). This template was created with the aim of facilitating the drawing of the pathways of oxygenation/deoxygenation in these new landscapes and then to connect the folded maze landscapes (cones) into one continuous model.

We began drawing hypothetical pathways on the new cone landscapes, which worked well (Figure 6.23). This provoked a discussion about the deoxygenated

FIGURE 6.22: Gemma Anderson-Tempini and Drawing Lab participants, photograph, 'Spiral pathway connecting via continuous cones', 2019.

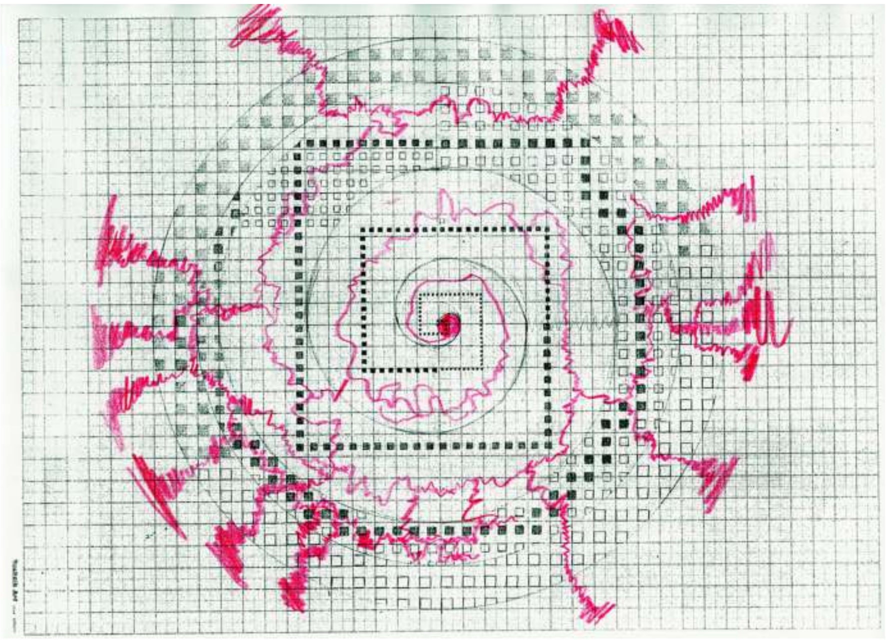


FIGURE 6.23: Gemma Anderson-Tempini and Drawing Lab participants, 'Drawing pathways on spiral landscapes'. Colour pencil and pencil on paper, 2019.

landscape, which Gemma had drawn with a tiny central area (stable state) graduating outwards to a large area (unstable state). We discussed how with deoxygenation haemoglobin moves from a location where it is stably oxygenated (the lungs) to an environment where it is stably deoxygenated (muscle). This meant that the grid Gemma had prepared actually needed to be inverted (coarse grain in the small area at the centre progressing to a fine-grained larger area at the periphery). We noted the changes that were required to the deoxygenated grid, so Gemma could revise the landscape once more. We continued to assemble the continuous paper model and introduce 'pauses' between oxygenation and deoxygenation to represent the stability of each fully (de)oxygenated state and the time taken to move the protein around the body. We discussed the nature of the pathway during the pause and agreed that the stable state would be maintained (and therefore we rendered the neighbourhood depicting the pause with fine granularity to represent the relative stability of this state). After recreating the pause element in this way by means of a paper extension to the maze, we decided that rendering this as a continuous area of the grid that is then cut and bent would be more elegant. By the end of our collaborative drawing activity, we had gained several helpful insights that moved forward our shared understanding: the area of the neighbourhood corresponds to entropy; the granularity to stability; the line that we draw on the maze to the energy of the molecule/protein.

Discussion

Collaborative drawing

The ability to construct shared meanings with peers during the drawing process improved both the group's social relationships and their approach to the research questions. The sessions gave rise to a 'group play' (Kukkonen and Chang-Kredl 2017) that encouraged shared meaning-making, and the combination of open-ended and guided (through the use of templates and parameter-based restrictions) drawing activity encouraged this more than purely open-ended activities. Participants established and maintained shared meaning through the use of shared common knowledge and applied various verbal and non-verbal communication strategies to advance their exploration. Not only was discussion used to define the various protein energy landscapes but it also continuously shaped the direction that the drawings took. As a result of the drawing process, including the discussions, some scientists created drawings that were complicated as well as carefully and clearly composed. The creation of shared meanings through drawing – a kind of intersubjectivity – can enhance social, cognitive and communicative abilities (Kukkonen and Chang-Kredl 2017). The meaning of the drawings was articulated collectively in the Drawing Labs. A shared focus of attention is needed to develop this intersubjectivity, which may be fostered through both metacommunication (verbally establishing common themes for drawings) and communication (discussing the content of drawings and providing each other with feedback as the drawing activity progressed) (Coates and Coates 2006; Cox 2005; Wood and Hall 2011).

Embodied practice and a new molecular aesthetic

Drawing Labs require embodied practice and an engagement with tangible media that, over time, refine scientists' aesthetic sensibilities, intuitions and judgements and train them to distinguish, and articulate, finer and finer differences in the phenomena. The drawings make visible previously obscured phenomena and disrupt scientific activity through interventions that may catalyze new ways of thinking, making and doing science: 'The pictures in the memory that have once made their way through the hand stick much more firmly in the head' (Hopwood 1999: 483).

Both the living processes and the models created during the Drawing Labs must be understood as dynamic phenomena that are subject to change as theories and experiments evolve. Analogies enlist imagination, experience and intuition to shed light on complex processes or otherwise imperceptible phenomena (Myers 2015: 162). Thus the drawing becomes a model and acts as an analogue of a protein, and each drawn model is a distinct embodiment of a modeller's knowledge about a specific molecular dynamic configuration or structural relationship (Myers 2015: 77). We wonder how this 'externalized' perspective and these practices of 'world-making' square with the 'inner' perspective of intuition. Drawing Labs make possible the drawing of these relationships that are hard to articulate through words.

Drawing Labs, and the focus on the drawing process itself, open the door to different kinds of aesthetics in scientific imagery. The process of drawing allows scientists to engage aesthetically with protein dynamics. The provision of a template structure helps the scientist get over the fear of the blank page, and thus removes a crucial obstacle to drawing for scientists who are not trained in this activity. Subtle differences, both in content and aesthetics, between the way members of the same research group draw the same protein, created a plurality of possible images to be discussed and understood. The images are collectively created, which raises interesting questions of who authors the aesthetic of the image and how to describe an aesthetic of co-creation. Rather than an aesthetic of communicative clarity, often emphasized by scientists and science communicators, perhaps we should rather aim for an aesthetic of working out, of testing and of iterative and progressive understanding.

In other words, what we have in mind is drawing as an interactive form of modelling that requires ongoing participation and opens up, rather than limiting enquiry, and leads practitioners into new ways of knowing (Myers 2015: 135). We think back to the use of yoga poses at the outset of this project, and to the parallels between body movements and protein movements they highlighted. This engagement with the phenomena being modelled contrasts sharply with the disconnection often associated with highly automated modelling or image-producing techniques. Drawing can, moreover, extend or expand what counts as a model or data. Drawings are not extra-scientific phenomena, they are (and could be more) intrinsic to forms of knowing and to enquiry in the field or the lab.

Recent discussion of models in the philosophy of science also includes a number of ideas that help to bring out the significance of our experiments in scientific drawing. Evelyn Fox Keller, for example, proposes a dynamic understanding of scientific modelling:

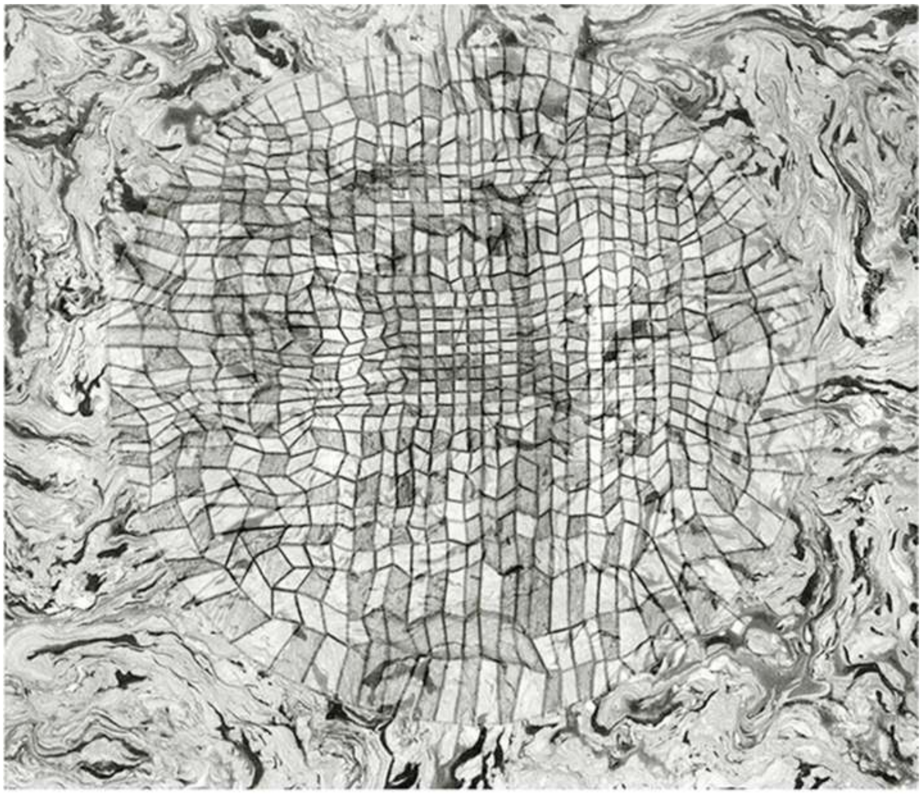
> The term ‘model’ is probably best understood as a verb, with the authors as subject, and the experiments and the conceptual schematic as a single, unparseable, composite object. Only at the end of the process do we have a separable entity – a model as a noun.
>
> (Keller 2000: 132)

If we think of ‘models’ as actions performed by modellers, then a protein model is not just an object at the end of the model-building process. Modellers articulate their knowledge of molecules through hands-on making, and in doing so they also imbue their models with their own sensibilities and intuitions (Keller 2000: 133). Moreover, philosophers distinguish many types of models, and between many elucidations of the term, such as Ian Hacking’s ‘models you hold in your hand’ and ‘models you hold in your head’. Hacking suggests that ‘[some] models are doubly models’: they are both representations of theories and phenomena (Hacking 1983: 216). This observation is especially pertinent to the present project. Certainly, the drawings generated in our Drawing Labs were intended to be representations of the process of folding. But the insights that emerged during the drawing process showed that they were also, and perhaps more importantly, vehicles for enhancing the researchers’ understanding of the target phenomena. During the iterative process of the Drawing Labs, earlier drawings could provide input into later versions.

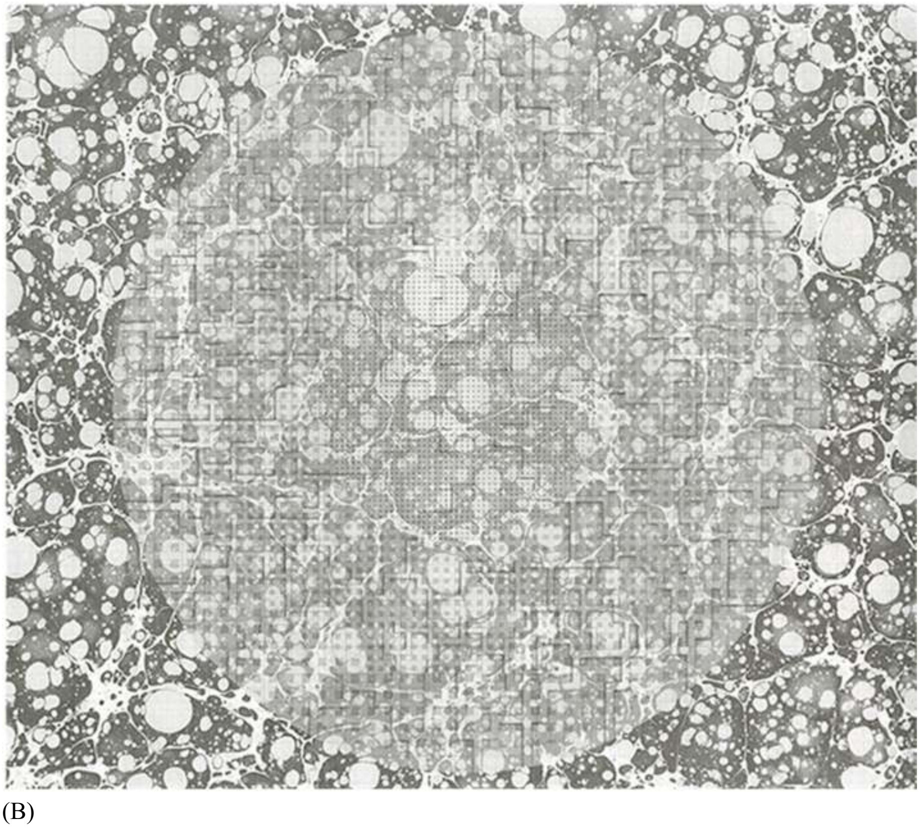
Reflections on how we draw boundaries and the continuum of processes

When two or more processes mutually stabilize each other, and hence both are responsible for the continued existence of the other, it can be difficult to determine where in their zone of interaction one process ends and the other begins. In our Drawing Labs, we were able to define a haemoglobin molecule as an individual process well enough. However, it remains unclear whether the surrounding water molecules, say, are part of this process or other processes interacting with 'it' (cf. insects and their obligate symbionts, such as Wolbachia [Dupré and O'Malley 2009]). This is an example of the natural tension that occurs in modelling and describing in simplified terms any continuum of processes. In the context of protein folding, the involvement of water is absolutely critical: it is considered the dominant influence on protein folding via what is known as 'the hydrophobic effect', favouring the formation of molten globules in partially folded protein intermediates and hydrophobic cores in natively folded proteins, for example. Arguably, in many of our drawings we are, in fact, creating and imagining 'fluid mazes' (Figure 6.24A–C). Although we did not fully develop the idea of a fluid maze, several group members found the opportunity to discuss this idea inspiring. The discussion also introduced them to the concept of 'the hydrophobic effect' which figures centrally in energetic explanations of protein folding. This is an example of how scientists readily engaged with an important concept in protein folding when drawing protein dynamics in a maze environment, and how this prompted intuitive exploration without much need for formal definitions and established theory.

Conceptually, then, looking at proteins as a kind of process inevitably raises the question of their boundaries. For many purposes, it is both natural and appropriate to draw the boundary traditionally assumed by chemistry around protein molecules (i.e. the molecule is defined as a continuous covalently linked set of atoms). The chemical bonds connecting the atoms within the protein are more stable than the bonds formed between the protein and the surrounding water. However, the folding process reminds us that the wider set of bonds between the constituent atoms in the amino acid chain changes as the configuration of the whole changes. Indeed, the geometry and various bonds (hydrogen bonds; disulfide bridges) continue to dynamically reconfigure during and after the nascent protein is folded – all inextricably linked to the surrounding water (in the case of a soluble globular protein). And there is no conceptual reason why these secondary bonds should be assumed to be more or less central to defining the whole than bonds to 'external' water molecules. So, at some point, a decision needs to be made on the extent of the process of interest, an abstraction motivated by the parameters of a particular scientific problem. A central advantage, but also a challenge, of process ontology is the insight that processes do not have the clearly defined and self-evident boundaries that mechanisms or things do. Indeed, as in the paradigm case of organism-level symbiosis,



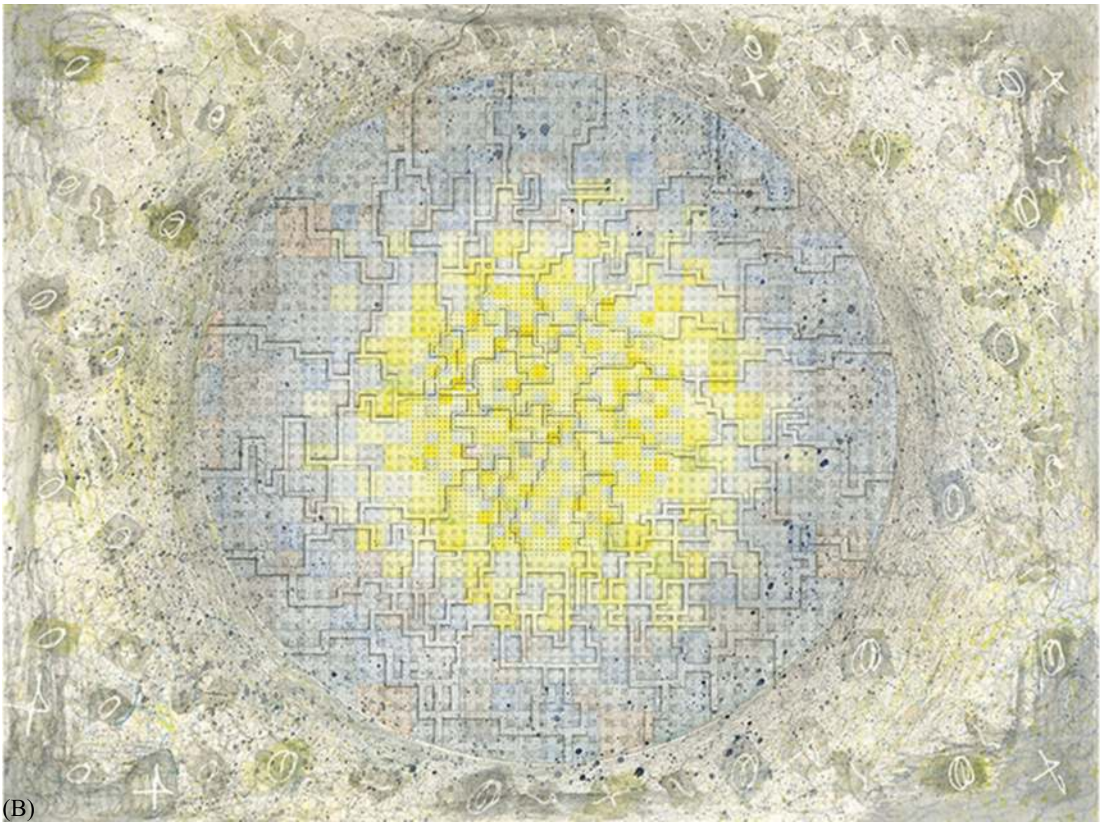
(A)



(B)

FIGURE 6.24A–C: Gemma Anderson-Tempini, ‘Fluid maze’. Pencil and watercolour on marbling paper, 2019.

FIGURE 6.24A–C: Gemma Anderson-Tempini, 'Fluid maze'. Pencil and watercolour on marbling paper, 2019.


(B)

we assume that relations between processes are partially definitive of the processes related. The drawing of boundaries within mutually entangled processes is always to some extent pragmatic, and the full understanding of such an abstracted process is never achievable without reverting to the consideration of its processual context.

In deploying the maze template, we have attempted to create a way of depicting processes in a way that reminds us of their embedding in biological and chemical contexts that partially determine their nature and behaviour. We are optimistic that this general template may be widely adapted to represent biological processes at a wide variety of scales.

Reflections on Drawing Labs and scientific method

Looking back at the drawing lab sessions, we now realize that each was ‘testing’ an idea and visual structure, and once we had reached a ‘result’ (i.e. a drawing that clarified our understanding), the result was copied (often using a photocopier); then further tests were undertaken on the copy until further results were established. There are obvious parallels between this process and the ways in which laboratory research progresses and drawing (typically of diagrams) is embedded in the work of scientific research groups. Each stage of an experimental project is both suggested and constrained by work that has gone before. In drawing, the drawer has to make frequent decisions about scientific subjects, and in doing so, drawing focuses on questions, while also allowing new questions to arise during the process. Drawing Labs have the potential to unify the vision of a research lab; as a vehicle for thinking together, sharing and developing a vision, drawing labs force the discussion to an abstract level that promotes thinking about the problem of representing processes. As this activity necessitates dialogue and involves thinking through the process of making that is outside normal scientific routine, drawing labs ‘disrupt assumed binaries between the intellectual and physical labour of research’ (Myers 2015: 16).

Drawing Labs provide a space and time for thinking carefully about scientific problems, amidst the business of lab work. In the act of drawing, the drawer must confront their own thoughts, images and ideas and share these with others, which can yield new insights for all involved. Drawing also allows for the comparison of images, the ‘before and after’, to see what has changed. The process of drawing, while grappling with the problem of representing protein processes, can give us a clearer understanding of what the protein is and what it does. The drawing process helps scientists to visualize and understand, to share with the group, and then to collectively build on that understanding. Drawing Labs are an interactive way of engaging with the nature of the multi-dimensional protein system, its developmental pathway and the process of depicting the energy landscape on a simple 2D sheet of paper. The Drawing Labs offered participants an intuitive way of engaging with the complex concepts of protein folding and functional switching and the intimate relationship between these biological processes and concepts of thermodynamics, kinetics, stochasticity etc. These typically require extensive formal training before they provide meaningful insight. Naturally, that formal training can come later, in the case of protein scientists, but exploration through drawing offers much scope for engagement in advance of such training. In Drawing Labs, we sought to transform latent scientific notions into images. But Drawing Labs also offer avenues towards the re-integration of drawing into scientific practice, through social and collaborative practice, as both inquiry and generator of questions, and as a way of synthesizing ideas and images.

Drawing Labs facilitate the rapid exploration of complex processes that are often represented via underlying formalisms that may impede exploration and intuition (both by requiring prior training and by slowing the process of creation). Through rapid creative exploration, Drawing Labs act as a vehicle for crystallizing questions and generating new knowledge. They cultivate and nurture the expertise and sensibility acquired during long training. Molecular vision is extraordinarily indirect; the 'human–computer lens' (diagrammed by Glusker and Trueblood 1985) and the technological lenses that draw proteins into view often disconnect. Drawing Labs provide an opportunity to imagine and talk about qualities of proteins that scientists consider vital, but that is difficult to communicate. In Drawing Labs, discovery through drawing is also a form of improvisation, a behaviour that brings the scientist closer to the nature of the protein as 'experience, improvisation, the utilisation of occurrences; it is an attempt in all directions' (Canguilhem in Myers 2015: 197).

Potential to impact scientific teaching practice

Drawing in science is traditionally emphasized as an individual form of investigation, research and representation. But little acknowledgement has been given to the benefits of group drawing. The Drawing Labs, however, showed that when scientists draw in the presence of their peers, they converse about and collaborate in the production of drawings. Scientists can develop and maintain shared meaning during group drawing. Reflection on our Drawing Labs suggests that the introduction of collective drawing activities could be fruitful, particularly where creative thinking, social bonding and problem-solving are concerned, in scientific higher education curricula as well as research. Drawing Labs are also similar to the discussions during meetings of scientific research groups, where collaborative drawing on the board might occur quite spontaneously. The teaching of complex biological processes is challenging. J. J. approaches teaching and learning by first attempting to cultivate intuition and then presenting formalism. In this vein, one could develop the Drawing Labs process into a vehicle for stimulating engagement and to impart an intuitive grasp of concepts prior to (or early in) formal instruction (e.g. protein folding thermodynamics and kinetics).

So far, however, we have primarily investigated Drawing Labs as a process that can change scientific practice and feed into a scientific protocol. We wanted to explore ways of better capturing the dynamic, processual character of living systems, and we believe that we have achieved some success with this. Moreover, the processual and interactive nature of the Drawing Labs also reflects the dynamic and relational nature of the biological objects under study, and this parallel holds out promise for exploring ways of better coordinating the dynamics of research with the dynamics of life. However, we are also interested in the drawing that is produced and the artistic insight this brings as well as how these new images can inform and inspire the artistic process (we aim to achieve an artistic process that has a true relationship to living/protein process).

The final aim was to use analogue drawing alongside computer/automated representations to enhance the scientific understanding of protein dynamics. Taking this further, we would like to test if the meaning of the maze images might translate to another research group who work on proteins, and also to a research group engaged with a different kind of biological process to see if the image could work as a metaphor for process in general. We are also interested in perspectives from the art community and how drawing can provide non-scientists with intuitive ways of gaining insight into biological processes.

Conclusions

Much of the visual material that we encounter in biology fails to capture the dynamic nature of biological processes in 2D images. Here, we have proposed that a collaborative approach that combines the methods of art and science can be used to produce novel biological images that represent higher dimensionality and dynamic movement. Art and science, therefore, can be understood as having the shared goal of discovering visual ways of exploring processes in complex systems and concepts. The thinking about processes that took place in the Drawing Labs also prompted a new awareness of research as a process. Extending scientific methodology in these directions is crucial in order to open up rather than foreclose what is possible to see, say, feel, imagine and know in today's life sciences.

Increasingly, the problem of moving from representations of objects towards representations of process is now also recognized by science. The images created in drawing labs also support the broader philosophical effort to find good metaphors and practices for representing, discussing and thinking about the process.

Metaphor plays an important epistemological and rhetorical role in scientific thought. The maze landscape functions heuristically as a visualization tool, as a metaphor for communication across disciplines, as a way of engaging scientists with visual thought and creative practice and as a guide for creating new models. Models and metaphors exist in the liminal zone between scientific theory and practice, and as Evelyn Fox Keller argues 'metaphors, like models, can themselves function as tools for material innovation' (Keller 2000: 77). The protein maze, moreover, contributes to a wider new understanding of the biological organization that stresses process and plasticity rather than fixed structure and genetic determinism.

Incidentally, this project provides a potential paradigm for addressing a problem that is a major concern growing out of work in process ontology, the possibility of an appropriate correlative process epistemology. From a process ontological point of view, any fixed representation is to some extent an abstraction from the process it represents. This is particularly problematic for processes of secular rather than cyclical change. This is strikingly illustrated recently by the difficulties in intervening in a viral pandemic in which the subject, the virus, is constantly evolving in ways partly driven by scientifically based interventions (social distancing and vaccination). The broader process ontological ideal would be to find a method of representation that is connected in an appropriately dynamic way to the changing phenomenon (Leonelli and Dupré 2022). Finally, we believe that the circular maze could function as a metaphor for processes beyond proteins and potentially provide the uninitiated with an interactive mode of exploring any process that can be modelled as a dynamic network with a global attractor.

Glossary

Gibbs free energy: This is a measure of thermodynamic energy in a molecular system that is available to do work. Rarely is the free energy calculated, rather differences are considered relative to some reference state. It is commonly estimated by its relationship to a chemical equilibrium constant (Eq. 6.1) or to enthalpy and entropy of the system (Eq. 6.2):

$$\Delta G = -RT\ln K_{\mathrm{eq}} \qquad \text{(Eq. 6.1)}$$

where R is the universal gas constant, T is the absolute temperature and K_{eq} is the equilibrium constant of the chemical process.

$$\Delta G = \Delta H - T\Delta S \qquad \text{(Eq. 6.2)}$$

where ΔH is the enthalpy, T is the absolute temperature and ΔS is the entropy of the system.

Maze: A complicated irregular network of passages or paths in which it is difficult to find one's way. The maze has many paths, whereas the labyrinth only has one.

NOTES

1. The denatured state of a nascent unfolded protein is conformationally diverse and so it has a very high degree of configurational entropy (given by $S = K_B \ln W$, where K_B is the Boltzmann constant and W is the number of accessible thermodynamically equivalent microstates), whereas the folded state is highly restricted in its structural dynamics and thus it has very low configurational entropy. Since protein folding is energetically spontaneous (i.e. favourable), it follows that this large loss of entropy must be compensated by a gain in enthalpy upon folding (since the Gibbs free energy of folding is given by $\Delta G_{(D-N)} = \Delta H - T\Delta S$, where ΔH is the change in enthalpy and ΔS is the change in entropy at temperature T). The folding pathway taken by the unfolded protein will relate to the available enthalpy gains and entropy losses at each step of the journey. For a detailed treatment of this topic see Fersht 1999).
2. Beyond the work discussed in this current chapter, we are developing 3-dimensional paper models of 4-dimensional reflexive lattice polytopes that allow us to better imagine the higher dimensional nature of the protein energy landscape and other processes.
3. Gemma contacted Professor Dame Janet Thornton (Director emeritus of the European Bioinformatics Institute, part of the European Molecular Biology Laboratory) and asked if she could describe something about the nature of protein movement using descriptive terms, diagrams and verbs. Here is Janet's response (12 September 2017):

> I am delighted that you are interested in proteins and their movements – they are the most beautiful molecules and perform all sorts of dances. For me I always think about motion in proteins at different levels & time-scales:
>
> Very small jiggles – that occur VERY quickly e.g. rotation of phenylalanine rings and surface side chains that occur faster than nano-second timescale
>
> Movements of loops – much slower, but very common
>
> Movements of domains – much slower, usually hinged around the connecting loop; but very important from a structural perspective. These are probably the most important functionally and are widespread – often in milli-second time scale or longer
>
> Movements involved in catalysis – small, often localised, but totally coordinated and evolved over billions of years evolution (we have some videos of these – which are very complex, but show the detailed movements in the active site of the enzyme) – a sophisticated ballet dance
>
> Completely disordered proteins – which are quite common and also have a clear functional role
>
> Formation of protein–protein complexes – i.e. gross movements towards each other. Some form permanent complexes; some transient
>
> Changes in structure during folding – this can take seconds or minutes

> Use of chaperone proteins to help folding, without getting disordered and entangled – this happens mainly by segregating chain in a chamber where it can fold ‘alone’.

4. A further resonance for the act of drawing the maze is the relationship to designing and folding the origami proteins.
5. Later we agreed to equate large (high) granularity to instability and fine (low) granularity to stability. There continued a discussion of whether this more accurately reflected entropy, rather than stability per se. This was ultimately a hotly contested topic within several drawing lab sessions, but serves to illustrate that the act and process of drawing was able to cultivate a common (often visual) language for the discussion of complex highly abstract concepts.
6. Proteins have biological activities which are often modulated, for example by the binding of another protein or a chemical: this is the basis for much of medical treatment. This up/down-regulation can be considered as a functional switch behaviour. A very simple case of this is myoglobin in muscle which takes up oxygen from the blood and so switches between an empty (deoxygenate) state and a bound (oxygenated) state.
7. Here, we use ‘Neighbourhoods’ to describe regions of equivalence in thermodynamic stability (or entropy, see note 4). Within a ‘neighbourhood’, we would anticipate the protein structural conformers to be accessible and to interconvert rapidly.
8. Here, we use ‘Bound State’ to describe the protein (haemoglobin) when bound to oxygen – one of its physiological ligands. Haemoglobin can bind between 0 and 4 oxygens simultaneously and does so in a cooperative manner.
9. The continuation of the creative thinking beyond the drawing lab session reflect the participants’ interest and engagement in the process.
10. We used the template to explore the following questions; What happens when you put the starting point at the outside of the maze and what is outside the maze? How can we think about boundaries? Can we represent different proteins as different pathways through the grid? The maze template generally has one centre/basin but all protein energy landscapes tend to have more than one centre, how can we experiment with ‘multi-basin cones’? How can the chaperone protein be represented? Can we conceive of the maze landscape as part of a web/matrix of connected landscapes? Could this be represented using a 4D tetrahedron (Figure 6.2).
11. Note that this was an intuitive exploration process and was not intended to be a quantitative model based on empirical data of relative thermodynamic stability between the stable states of the proteins considered. The potential for such drawings as these to be used as a quantitative representation of experimental and/or simulated data was discussed and is of particular interest to all of the scientists that participated in the drawing labs. However, it was out of scope of the current study.

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7

Drawing Out the Superorganism: Artistic Intervention and the Amplification of Processes of Life

Heather Barnett

Introducing the superorganism

> *[In] trying to understand systems that use relatively simple components to build higher-level intelligence, the slime mould may someday be seen as the equivalent of the finches and tortoises that Darwin observed on the GaIápagos Islands.*
>
> (Johnson 2001: 12)

As one of around 900 known species of slime mould, *Physarum polycephalum* can usually be found creeping around the ground vegetation of temperate woodland. Comprising thousands, often millions, of individual nuclei, all operating as one single entity, the slime mould is considered a superorganism – a collective organization of individual elements working in highly coordinated ways. Within the superorganism, a dynamic network of interconnected tubules helps distribute nutrients across the cell mass, as well as communicating valuable information about environmental conditions. Among its listed achievements are high-level network optimization (Nakagaki et al. 2000, 2001), spatial and temporal memory (Saigusa et al. 2008), the ability to learn from its environment and to pass that learning onto other slime moulds, even after lying dormant for more than a year (Vogel and Dussutour 2016). It is therefore little surprise that, outside of its natural habitat, the slime mould has become a valuable model organism, serving diverse fields of enquiry, from biophysics to computer science, from urban planning to philosophy and from material science to music and art. In laboratories and studios across the globe, researchers are asking questions of the slime mould, seeking to better understand how such a simple organism can achieve such complex tasks.

The work under discussion here is a series of time-lapse film studies made between 2009 and 2018, working with *Physarum polycephalum* within a studio environment, introducing the organism to novel environments and capturing its growth trajectories as it navigates: calculating routes, making decisions and responding to encounters (Figure 7.1). The films are part of a larger ongoing artistic inquiry, operating under the umbrella title of *The Physarum Experiments*, which connects slime mould and human ontological sensibilities through

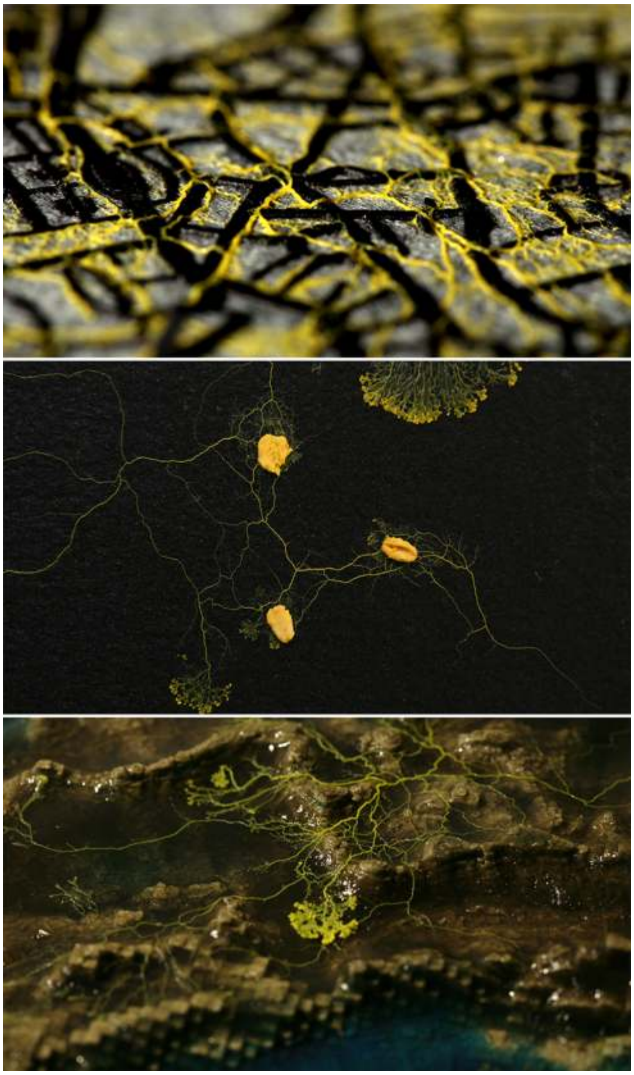

FIGURE 7.1: Still images from the slime mould studies *The Physarum Experiments*. © Heather Barnett.

a range of media and employs hybrid (artistic and scientific) methods. The varied approaches – including the co-creation of experiments, artworks and experiences – seek to draw connections between disparate life forms and create interspecies encounters (Barnett 2019a, 2019b, 2021). My interdisciplinary artistic practice, developed over several decades, involves working directly with living systems, seeking to reveal behaviours which operate beyond human perception. Mediated by imaging technologies, such as microscopy (spatial magnification) or time-lapse photography (temporal magnification), technological intervention aids in a relational exercise, permitting access to other processes of life.

Subjectivities of time

> *Whatever the relations between a subject and the objects in his environment, they always take effect outside the subject, and that is where we must look for the perceptual cues.*
>
> (Uexküll 1934: 327)

As with all organisms, the slime mould operates in the world according to its unique sensory characteristics and physiological capabilities. Its subjective realities are predicated on its species-specific relationship with its surroundings, which operate distinctly but in concert with a multitude of interrelated subjectivities. In his seminal 1934 essay, *A Stroll through the Worlds of Animals and Men: A Picture Book of Invisible Worlds*, naturalist Jacob von Uexküll identifies all creatures as ‘subjects’, not ‘machines’, operating through a complex and highly individualized interrelation of perceptions and actions. By moving away from mechanistic ontological interpretations, ‘We thus unlock the gates that lead to other realms, for all that a subject perceives becomes his perceptual world and all that he does, his effector world. Perceptual and effector worlds together form a closed unit, the Umwelt’ (Uexküll 1934: 320).

An organism’s Umwelt, literally meaning ‘surrounding world’, is based on its body size, its sensory processes and its metabolism – consider the olfactory realm of the dog, the haptic exploration of the octopus or the pheromone landscape of the ant colony. According to Uexküll, the key factors in how an Umwelt operates for any individual organism relate, not only to their inherent biochemical, physiological and cognitive processes but to the spatial configuration of their body plan in relation to their environment, how time behaves in the organism’s world and how individual moments are experienced within the body.

> Time as a succession of moments varies from one Umwelt to another, according to the number of moments experienced by different subjects within the same span of

> time. A moment is the smallest indivisible time vessel, for it is the expression of an indivisible elementary sensation, the so-called *moment* sign.
>
> (Uexküll 1934: 340)

Arguing against any unified definitions of lived experience, he calculates that humans operate at a 'moment time' of one-eighteenth of a second, drawing on empirical studies demonstrating that the human ear hears eighteen air vibrations in one second as a single sound or feels eighteen taps per second on the skin as continuous pressure. This he compares to equivalent studies indicating a 'moment time' of a quarter of a second for snails and one-thirtieth for fish, based on similar observational experiments (Uexküll 1934: 341). Based on my own empirical understanding of the slime mould, I would calculate its 'moment time' as one beat per 90 seconds, in line with its rate of protoplasmic streaming (Barnett 2013b), the rhythmic pulse of growth that directs all motion of the organism (Figure 7.2).

What is of interest in my own visual enquiry is the relationship between the lived experience of time and the representation of time through technological mediation, specifically, how the rhythms of life can be amplified from slime mould to human spatio-temporal scale. As an image-maker working with differing organisms' moment times, the question is how to translate those shifting scales of perception into moving image – how to capture, render and represent the rhythm of life and growth in motion. If humans operate at around one-eighteenth of a second frequency, it follows that they perceive movement at the same base rate, so any moving image screened at eighteen frames per second (fps) or above will be perceived by humans as natural motion. Commonly, film and video are screened at 24 fps and more recently at 30 or 60 fps or higher as technological developments allow for better resolution and faster frame rates. The logic, therefore, would follow, that films made for an audience of snails would be screened at four fps to appear convincingly 'real' to a snail audience and for slime moulds at around one fps or slower.

Despite the obvious nonsensical limitations of making moving-image entertainment for organisms that operate in an olfactory or chemosensory – and non-visual – world, speculative enquiry has its value. Supporting his investigations into the relative subjectivities of organisms, Uexküll utilized imaginative visualization as a form of speculation. His studies were illustrated with drawings and altered photographs depicting how a given organism 'sees' the world; for example, a village street scene as seen by a human, a fly or a mollusc (Uexküll 1934: 335). Of course, the accuracy of any such representation is questionable. Even if we have a physiological understanding of how a bird visually perceives the world based on its optical and neurological make-up, we cannot know with any confidence how it understands what it sees, spatially or conceptually. What Uexküll offers us in his representations,

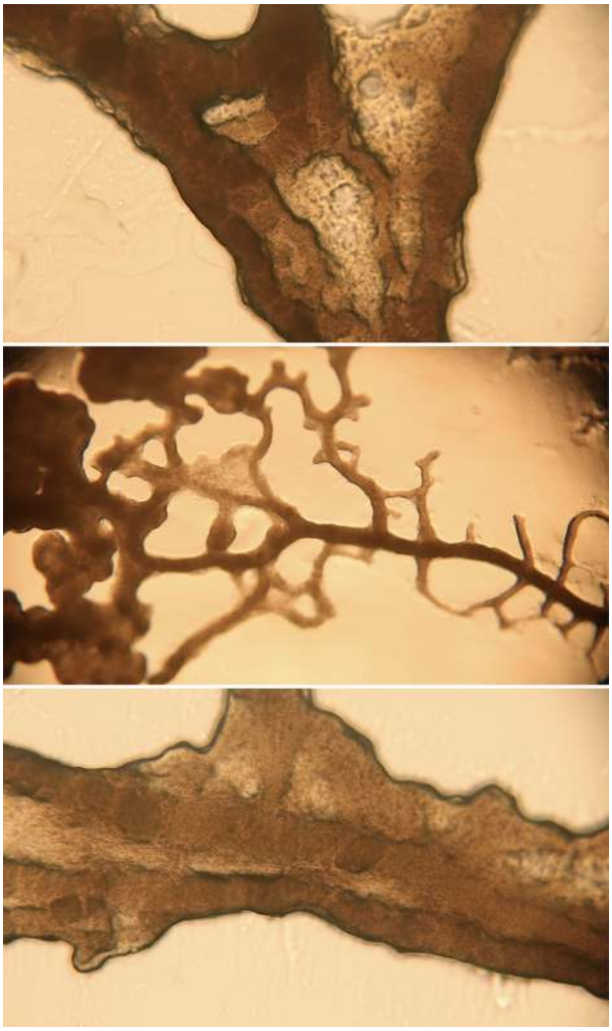

FIGURE 7.2: Still images from *The Physarum Experiments, Study No.020: Streaming*, showing the flow of nutrients and chemical information within the network of dynamic veins (2013). © Heather Barnett.

and what I offer in my film studies, is a visual 'potentiality of experience' (Elkins: 96) inviting the viewer into another realm of sensory and temporal perception.

In my investigations, I use cameras and computers to transcend the temporal worlds of human and slime mould. I am interested in how we perceive the passing of time in our own world (in mind and body) and the relative subjectivities of time through human/slime mould speculation. Through the representation of growth trajectories and behavioural responses to given interventions, I aim to '*draw out*' fundamental processes of life and use technological mediation – specifically macro and time-lapse photography – to create a relational encounter.

Perceptual processes

> *We must recognize that Nature itself is always in movement, in process, and under construction.*
>
> (Shaviro 2016: 216)

The slime mould's Umwelt is one of biochemical sensing, navigating its world through chemotaxis. As the organism roams, it is constantly interpreting the chemical signals it discerns, homing in on food sources, avoiding toxic repellents and recognizing its own chemical trail left behind in earlier journeys. Signals are distributed through the body of the organism through a process of protoplasmic streaming, a rhythmic flow of nutrients and chemical information pulsing inside a dynamic network of interconnected veins. Its physiological properties are driven by protein dynamics, actin and myosin contracting and releasing – the same proteins activating human muscular motion – enabling it to pulse in multiple directions simultaneously (Nakamura and Kohama 1999). The supercell is held together by a mucus membrane containing a multitude of individual nuclei shuttling around within. Its body is a shape-shifting network, always fluid, ever-changing in response to its surrounding world. It is a nomadic environmental barometer, highly sensitive to changes in temperature, humidity and chemical composition. It can also detect changing pH in its environment, which manifests in a morphological colour change from bright yellow to darker orange (Seifriz and Zetzmann 1935).

These dynamic processes give rise to particular growth patterns: branching out whilst foraging (to maximize coverage of territory) and forming networks once nodes have been established (to strengthen connections and facilitate the transfer of information). Branching is a fundamental strategy within myriad biological organisms and physical phenomena, from the bifurcation of river deltas, lightning strikes, tree roots and branches, to mycelial networks and in our own bodily systems including blood vessel networks and the cross channelling of neural pathways. Branching facilitates 'the transmission and parsing of information, no less than the transfer and dissipation of energy' and, according to philosopher Stephen Shaviro, 'is an essential process of Nature' (2016: 220). Taking advantage of the affordances offered by its physiology and the sensory ecology of its Umwelt, '*Physarum polycephalum* continually prods, pokes, and provokes its environment. It navigates and searches, oozing and flowing and extending itself through its surroundings' (Shaviro 2016: 213). As such, the slime mould is an oscillatory information processing and distribution system, operating within a constant feedback loop of communication 'from its encounters with objects, fields, and energy flows all around it' (Shaviro 2016: 214). And it is these same flows which I aim to harness in my own interventions with slime mould processes.

For Shaviro, 'information processing mediates between perception and action' (2016: 220) and forms the basis of fundamental sentience within the natural world. He does not suggest that organisms such as trees or bacteria are conscious, but he does argue that 'they are demonstrably sentient, as they process information and respond to it in ways that are not stereotypically determined in advance' (Shaviro 2016: 221). This unconscious information processing, not entirely dissimilar to the extensive subconscious neural activity within our own brains, gives rise to unpredictable and nuanced responses to changing environmental conditions. It is far from mechanistic and allows the organism to recognize the significance of signals and make decisions about what to do next. The many admirable attributes of slime mould are an emergent property of the multitude of interactions within the superorganism and between its body and its environment – a dialogue between a many-headed organism and its world.

In the films I create, I aim to bring together the conceptual, biological and aesthetic properties of 'slime mouldness' through the staging of the organism within constructed environments and the capturing of its biological actions and reactions through time-lapse photography. Here, time is manipulated outside of the confines of any species-specific 'moment' time and enters an intermediary space between human and slime mould rhythm and flow, drawing the two realms together. The 'moment' of time-lapse photography is one which can encompass these relative subjectivities of time. Time itself becomes a medium by which to translate processes of one life form to be better understood by another.

Playing with time

> *The 'revealing "eye"' of the microscope and the 'analytical "brain"' of the camera were described as active observers: by portraying the aliveness of the world, technology itself came to life.*
>
> (Field et al. 1942: 52)

There are certain practical challenges to overcome in photographing slime mould, an organism that does not like light and that moves very slowly. Too much light alters the slime mould's physical state, forcing it to switch from a continuous growing plasmodium into a fruiting body containing spores. Growth-wise, its top speed is around one centimetre an hour, depending on a number of interconnected variables such as humidity, temperature and relative states of hunger – for example, it slows down when too cold or too dry and increases fluctuations when it finds food. These growth characteristics are imperceptible to human observation in 'real time'. Therefore, imaging technologies – in particular time-lapse photography – are employed as a means of amplification and translation. This mediation involves the capture of individual still images at regular intervals. Shooting over hours, sometimes days, the numerous stills are then composited into a continuous moving image, recombining instances at a fast enough frame rate to represent perceivable motion. Humans perceive movement convincingly at 24 frames per second (or as stated previously, according to Uexküll's experiments, at a minimum of eighteen). The fast succession of images creates the illusion of natural motion so that the viewer is perceptually convinced of its authenticity.

Capturing the processes of life in motion has a long history, dating back to early twentieth-century cinematographic innovators such as Percy Smith, who pioneered time-lapse and microphotography. His inventive films presented the behaviours of organisms as never seen before, producing an eclectic filmography throughout his career. As part of a team working for British Instructional Films after the First World War, he contributed greatly to a series of natural history films, *Secrets of Nature* (1922–34), which depicted vernacular views of plants, animals, birds and insects (Long 2020). As part of this series, he captured the slime mould in *Magic Myxies* (Smith and Field 1931), a ten-minute black and white film which reveals the curious characteristics of slime mould, here defined as both animal and vegetable. Despite this taxonomic inaccuracy (slime moulds have also been classified as fungi and are now settled within the kingdom of the amoeba) and the amusing anthropomorphism at play in the typically 1930s BBC narration, the film depicts the full complexity of the organism's life cycle and physiology, including spore dispersal, plasmodial migration and fusion. The granular detail of protoplasmic streaming is also depicted and described, as a channel pulsing forward and backward, 'this ebbing and flowing causes the Myxie to advance like the sea, in waves' (Smith and Field: 1931 04:10).

The influence of filmmakers such as Smith, and the form of biological representation they pioneered, can be seen in the development of natural history filming over the last century. The BBC Natural History Unit has produced incredible footage of slime moulds growing in their (seemingly) natural habitat, traversing logs and consuming mushrooms (*Autumn* 2013). More recently, films such as *The Creeping Garden* (2014), a feature-length documentary, have placed the slime mould – and the people who work with them – centre stage in innovative ways. And in 2016, *Magic Myxies* was re-visited by musician Stuart Staples, who re-cut Smith's microscopic footage accompanied by a 'sometimes soothing and often sinister' (Barkham 2016: n.pag) instrumental score. *Minute Bodies: The Intimate World of F. Percy Smith* is an 'interpretative edit' which creates 'a hypnotic, alien yet familiar dreamscape that connects us to the sense of wonder Smith must have felt as he peered through his own lenses and seen these micro-worlds for the first time' (Brown 2016: n.pag.).

Questions of representation fall into technical, communicative and ethical dimensions. The perceived status of the organism may be affected by the choice of camera angle, scale and viewpoint, how it is framed and with what contextual information in relation to surrounding circumstance. These in-camera decisions, along with other factors relating to interval time and editing decisions, combine to form a representational assemblage which portrays the processes of life. There is also a question of intervention, i.e. to what extent the filmmaker interferes with the biological processes in order to maximize the drama of natural events. Most contemporary natural history filmmaking follows a strict line of non-intervention, the film-makers role being merely to observe. In contrast, Smith's early films involved the glueing of a fly onto a tiny chair so that it could juggle a ball with its legs. In my own time-lapse studies, I take the organism out of its natural habitat and into constructed environments, but with some consideration for the wellbeing of the organism. Knowledge of environmental preferences and biochemical responses, coupled with time subjectivities, enable me to create the conditions for the slime mould to reveal itself and form its own biosemiotic language.

Learning from – and with – the organism

> *Many of the processes we might consider fundamental features of the brain, such as sensory integration, decision-making and now, learning, have all been displayed in these non-neural organisms. The survival of slime moulds depends on their ability to respond and adapt to changing environmental conditions.*
>
> (Boisseau et al. 2016: 6)

My own early time-lapse studies were an ad hoc exploration of what was happening in slime mould time. Initial experiments introduced the organism to various food sources including plants and desiccated insects, as well as known culinary favourites such as oat flakes. I grew it on a range of substrates including coloured agar gel, wet felt fabric and velvet covered in agar – in fact, any material that would hold moisture and provide a suitably humid environment (Figure 7.3). Through these early studies, I observed an array of intriguing behaviours and growth formations and whilst I could predict certain responses, the slime mould would not always conform to my expectations. It was clearly following its own behavioural logic, but I could influence its trajectories to some extent through the placing of attractants or repellents or by altering environmental conditions.

My understanding of the organisms' preferences and their underlying physiological mechanisms grew through a combination of empirical study, coupled with

FIGURE 7.3: Early studies experimenting with different food sources and substrates. © Heather Barnett.

explicit knowledge gleaned from the abundant scientific papers – there are over 67,000 published academic papers on slime mould cited on Google Scholar. For example, in *Study No. 011: Observing growth over 136 hours* (Barnett 2009), having fed on a pile of oat flakes the slime mould set off exploring, two 'heads' setting route simultaneously. As the two branches extended across the terrain, they gradually grew towards each other and, prior to the meeting, the entire organism paused in its tracks and shifted its direction of flow in search of novel foraging territory. Before the point of physical contact, the slime mould recognized that it was already there and changed its course of direction (Figure 7.4).

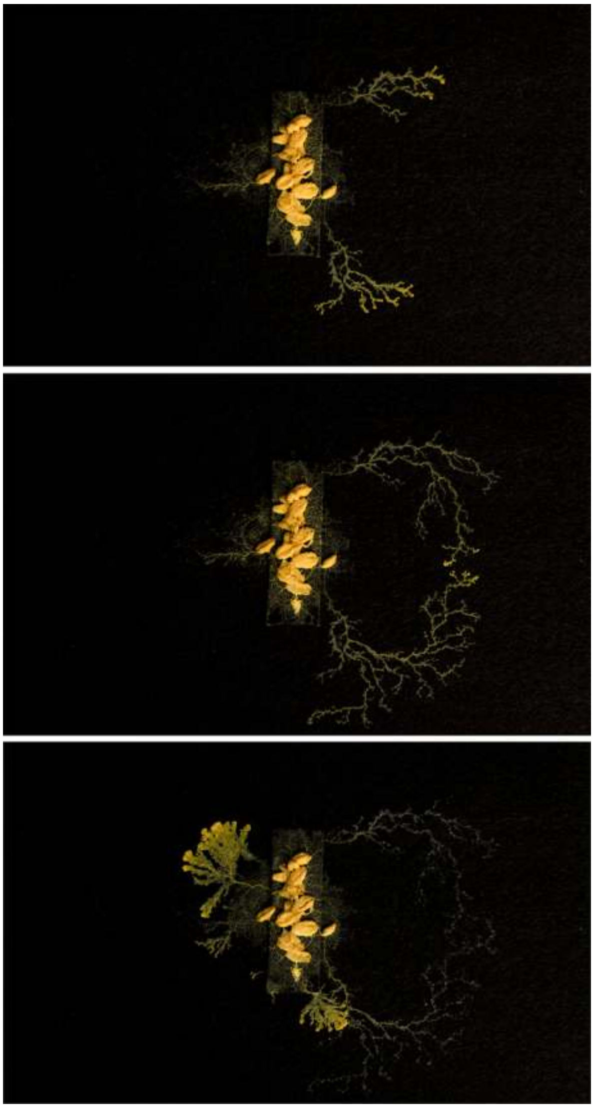

FIGURE 7.4: Still images from *The Physarum Experiments, Study No. 011: Observing Growth over 136 hours* (2009). From top-down: growth trajectories; point of recognition; change of direction. © Heather Barnett.

This form of self-awareness, known as allorecognition, enables the organism to identify 'self' from 'non-self' in its environment. In slime mould, this function is facilitated by an extracellular sheath extending from the membrane of the super-cell, which enables it to initiate fusion or to avoid repellents (Masui et al. 2018). This 'self-extension model' identifies chemical information transmission through direct physical contact and through airborne molecules enabling the organism to transmit information about itself into the world (Masui et al. 2018: 7). In *Study No. 011*, non-contact recognition of self was demonstrated as the two slime mould 'branches' converged on one point, allowing the organism to alter its flow of energy and change direction of travel.

Allorecognition can also be seen at play in later time-lapse studies, in the fusion of genetically identical slime mould cells and in the avoidance strategies of two species of slime mould in an enforced encounter. This chemical recognition of self and other when seen through the amplification of time-lapse photography suggests seeming intention in the organism's decisions and trajectories. This function plays a significant role in its navigational abilities, as it deposits a trail of extracellular slime indicating where it has been and helping it to make decisions about where to go next – a form of externalized spatial memory, which is also affected by the complexity of the environment (Smith-Ferguson 2017) (Figure 7.5).

In addition to spatial memory, the slime mould possesses a form of temporal memory, demonstrated in a scientific study where the slime mould was exposed to cold dry air at regular intervals. The change in atmospheric conditions was not conducive to the slime mould and, as a result, it slowed down its growth in response to the unfavourable conditions (Saigusa et al. 2008). Once a pattern was established, the slime mould slowed down each time it felt the cold air, the researchers did not change the atmospheric conditions at the allotted time, yet the slime mould slowed down in anticipation of the event. Somehow the slime mould, without any sensory organs or central nervous system, was able to hold time-sensitive information about an expected event and adapt its behaviour in anticipation of its occurrence. The results of this experiment set out further questions about how the organism was capable of remembering, learning from and predicting events.

The research into slime moulds is vast and multi-disciplinary. From the fields of biochemistry, biophysics and computer science to urban planning, architecture, management theory and philosophy, research relates to questions of information distribution, adaptive networks, self-organization and collective coordination. Much of the recent work, undertaken over the past twenty years – both within and beyond scientific fields of study – was inspired by a seminal paper whereby the slime mould was tasked with solving a specific navigational problem of a maze. In 2000, a team of scientists at Hokkaido University in Japan designed an experiment to test the networking efficiency of *Physarum polycephalum* (Nakagaki 2001). They constructed a maze and filled it with sections of the plasmodium, which spread and conjoined into a single mass cell. Food was then added at two points in the maze and the organism was observed as it contracted to form a thick tubular network connecting the two nutrient sources. The organism retreated from empty areas of the maze, gradually rationalizing its form to a single dominant connective thread, taking the shortest and most efficient pathway. The

FIGURE 7.5: Extracellular slime trail forming an externalized spatial memory, helping the slime mould to navigate its environment. © Heather Barnett.

experiment, led by Toshiyuki Nakagaki, concluded that 'this remarkable process of cellular computation implies that cellular materials can show a primitive intelligence' (Nakagaki 2000: 470), thereby sparking much-heated debate amongst the scientific community about how 'intelligence' is attributed and how it is defined in organisms without a brain. Whilst there is still much to establish about how the slime mould performs beyond the sum of its parts, it is widely held within the scientific community that the source of the slime moulds' myriad capabilities is the frequency of oscillations within the process of protoplasmic streaming, a rhythmic and dynamic force.

Staging the organism

> *The Body without Organs is that glacial reality where the alluvions, sedimentations, coagulations, foldings and recoilings that compose an organism – and also a signification and a subject – occur.*
>
> (Deleuze and Guattari 1987: 159)

Engaging with the scientific literature helped underpin and inform my empirical learning and corroborated what I was observing directly from the organism. The scientific methods and research findings also inspired my artistic experiments, albeit in a non-hypothesis-driven way. My motivation was not to replicate the scientific experiments but to use them as a springboard for a more open-ended and exploratory form of enquiry, a staging of the slime mould, creating the conditions whereby the organism could reveal itself through my intervention. For example, my homage to the maze experiment, *Study No. 019 The Maze* (Barnett 2013a), took the form of a large Perspex three-dimensional maze set in a blacked-out chamber (to maintain favourable dark environs). Using the original maze design as a starting point, my replica scaled up and elevated the experimental terrain. In contrast to Nakagaki's experiment, the slime mould in this maze was encouraged to roam freely in search of food (Figure 7.6). I was interested in observing its growth trajectories as it navigated pathways – how it occupied the space – and how it would decide on a given path when presented with a choice – whether one 'head' would dominate or the organism would split into two to optimize potential finds.

In exhibition, when *Study No. 019 The Maze* is screened, it is often accompanied by the sculptural maze containing a live slime mould. This offers the viewer an opportunity to experience the living organism in action though, at a top growth speed of about one centimetre per hour, this requires considerable patience and close nuanced observation. The frustration inherent within this act of viewing becomes part of the exercise, however, to give contrast between the spectacle of the slime mould writ large on-screen, its behaviour accelerated and amplified through time-lapse photography, and the real organism slowly creeping around the maze looking for nourishment. It is an attempt to bring the human viewer a little closer to the slime mould's temporal existence, to create a small perspective shift.

Other environments I have constructed for slime mould exploration include the creation of moistened felt, velvet or paper substrates, 3D-printed terrains poured with coloured agar, petri-dish-scapes cast in agar and the application of various combinations of artistic techniques such as paper embossing, carving, laser-cutting and sculpting. These scenarios invite the slime mould to explore, navigate and encounter within a constructed environment, one that is artificial but made with the organism's needs in mind. The rationale to situate the experiments within

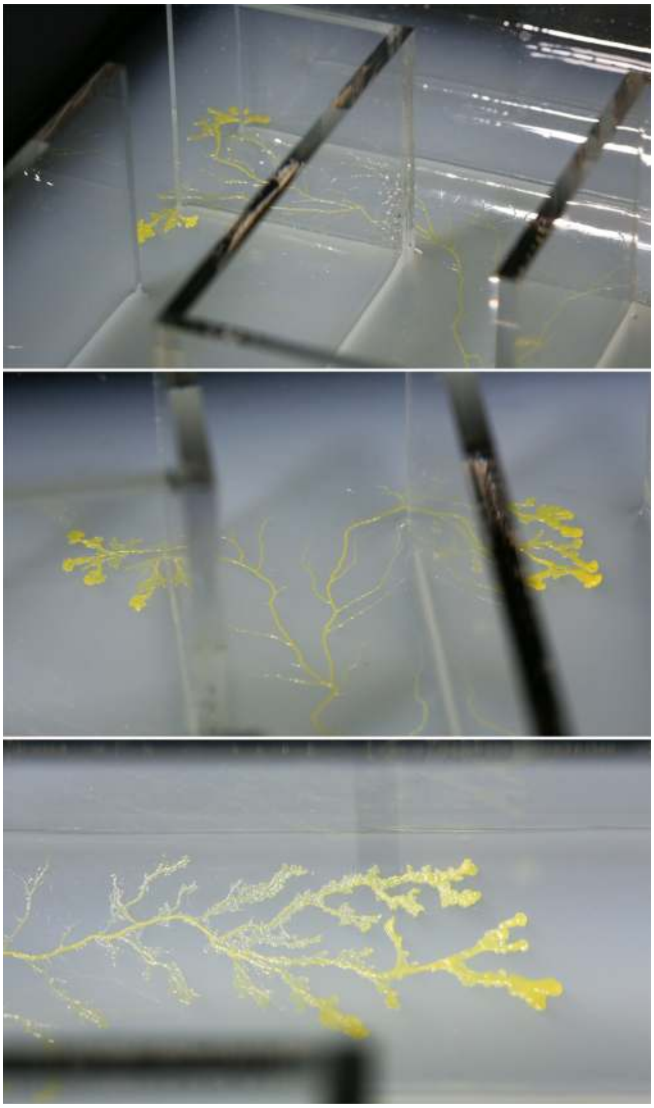

FIGURE 7.6: Film stills from *The Physarum Experiments, Study No. 019: The Maze* (2013). © Heather Barnett.

such a non-natural environment is multifaceted. On the one hand, to shoot in a studio/lab environment offers a degree of control over environmental conditions – I can maintain levels of light, humidity and camera position, which would be difficult to maintain in a natural environment. But it is not purely a pragmatic choice. The environments I construct lack any specific context and are devoid of any indicators of scale. Nor do I publish the time ratios at play within individual films, indicating the interval rate of shooting or the frame rate of playback. It is hoped that, by avoiding any scientific or natural history signifiers in the frame, the resulting ambiguity will draw the viewer in to decipher the structural behaviour and patterning properties for themselves – to speculate on what they are witnessing. The lack of explicit knowledge presented is intended to elicit a more tacit and experiential engagement with the processes of life at play.

By providing conducive environmental conditions and utilizing known attractants and repellents, the behaviour of the organism and its resulting growth trajectories are influenced by human intervention. Responses to given stimuli can often be predicted but can never be controlled. The slime mould will find all manner of interesting strategies for evasion, access or subterfuge and the results are often surprising. For example, in *Study No. 022* (Barnett 2016a), midway through an exploratory experiment I removed all food from the environment. Knowing that the slime mould was able to detect food from some distance (not solely through direct contact) I was curious as to how it would respond to the sudden change in the availability of resources. The resulting trajectories were flamboyant, the slime mould shooting out dramatically in a wide array of branches, the overall effect resembling a firework display (Figure 7.7).

Here, the relative states of hunger/satiation became part of the experimental setup. If there is too much food in the environment the slime mould will merely sit and digest it, which, depending on the number of oats provided, could take several days. If too hungry, it will not have the energy to 'perform' for the experimenter, so balancing this state is a key element to slime mould experimental design. Generally, a well-fed slime mould placed in a novel environment will generate a successful slime mould experiment. With no chemical traces from prior activity to distract it and with lots of energy pulsing around its veiny plasmodial body, an interesting response is likely to occur.

It is not only the environmental conditions that influence what behaviour is represented through time-lapse photography. The space of intervals between each photograph taken significantly affects the spatial representation and what aspects of physiological response are made evident. For example, to demonstrate the pulsing mechanism of protoplasmic streaming, the interval rate should be no more than 60–90 seconds, as that is the time it takes for the direction of flow to shift direction. To view more dynamic global trajectories, a less frequent interval rate should be adopted. For example, the dramatic effect of the starvation fireworks was shot at an interval rate of one frame every three minutes over a period of several days, compared to the maze navigation which was shot at an interval rate of one frame every twenty seconds, over several hours. In the latter, the rhythmic flow of protoplasmic streaming is clearly visible.

In another experiment, *Study No. 024: Interspecies Encounters*, I introduced two species of slime mould into an environment equidistant to a food source (several oats placed in the centre of the dish) (Barnett 2016b). In addition to *Physarum polycephalum*, my regular 'collaborator', this experiment also involved a

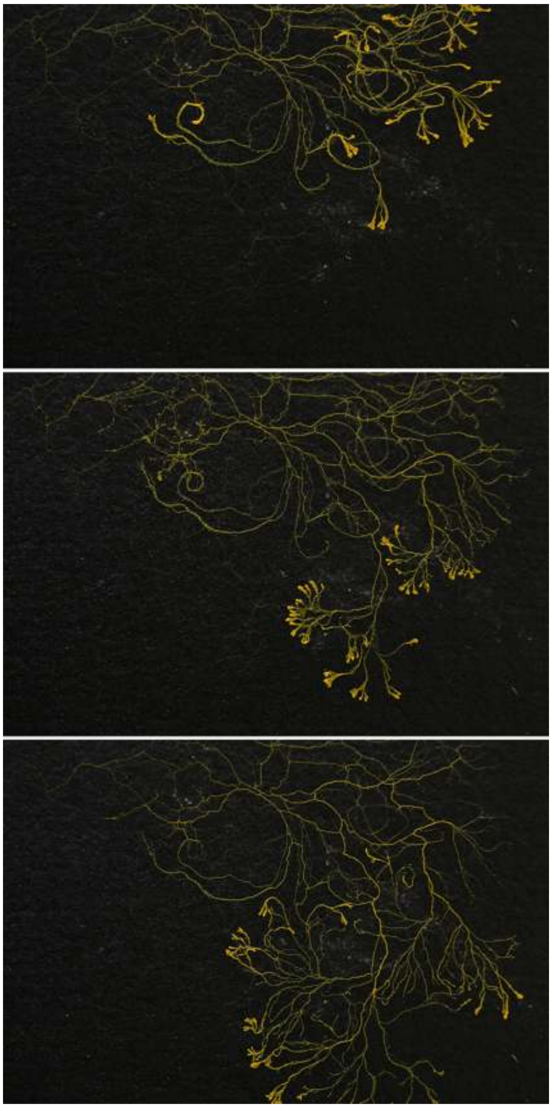

FIGURE 7.7: Film stills from *The Physarum Experiments, Study No. 022: Starvation Fireworks* (2016). © Heather Barnett.

Danish species of plasmodial slime mould, *Badhamia*. Whilst the two organisms share general physiological behaviours, the characteristics revealed here are highly individualized: *Physarum polycephalum* bifurcating long distributed tentacles, whilst *Badhamia* forming a dominant driving force pulsing towards the other slime mould.

As the time-lapse evolves, the *Badhamia* pushes forward, past the oats (not *Badhamia*'s favourite food it turns out), intimidating the *Physarum polycephalum* into retreat, forcing it to change tack and forage in other directions – a battle clearly won. However, on closer inspection, it is possible to detect a small offshoot of *Physarum polycephalum* which has taken refuge behind an oat as the *Badhamia* wall of attack passes by (Figure 7.8). A satellite slime mould had broken off from the retreating main body and taken evasive action, avoiding detection by the other more aggressive organism.

What I describe here is akin to interspecies warfare strategies and suggests a pre-emptive form of action, weighing up the relative attraction of food vs. the hostility of the other organism. This might seem like an anthropomorphic projection of human sensibilities and cognitive reasoning onto a single-celled creature,

FIGURE 7.8: Film stills from *The Physarum Experiments, Study No. 024: Interspecies Encounter* (2016). © Heather Barnett.

but this attribution is supported by the scientific literature. There are numerous papers on decision-making which analyze variable cost/benefit trade-offs (Beekman and Latty 2011, 2015; Reid et al. 2013, 2016) and, despite the caveat of anthropomorphization, it is hard to dispute that *Physarum polycephalum* took evasive action in direct response to the other organism's presence, position and direction of movement. Its response is a combination of multiple minute calculations assessing what was happening at that moment and what might happen next.

The final example to include here, *Study No. 026*: *Intraspecies Fusion*, introduced two genetically identical slime moulds in an abstract landscape (Barnett 2018). The environment is cast in black agar, a mixture of agar powder and squid ink powder to provide a nutrient-rich and high-contrast background. The two organisms are placed in the environment a few inches apart. As they explore their new territory they pulse towards each other. After a gradual approach, there is a moment of hesitation before physical contact is made, immediately followed by a fusion event – a tubular network forming across the divide (Figure 7.9). As observed by Percy Smith in his film, *Magic Myxies*, 'when two myxies meet they immediately join forces and flow away together' (Smith and Field: 1931: 04:45). Where there were two organisms, there is now one – perfectly integrated and operating as a single entity. Much recent scientific research has focused on the process of this fusion, particularly in relation to questions of learning and protocognition. Experiments have demonstrated that the act of fusion, not only conjoins cellular matter but enables slime moulds to pass habitual learning (learning gleaned from its encounters with its environment) onto other non-habituated slime moulds (Vogel and Dussutour 2016; Vallverdú et al. 2018), the organisms' exchanging and merging chemical knowledge about their surroundings.

Definitions of intelligence are now expanding to embrace non-neuronal forms of cognition across many living systems which embody environmental dialogue, organism reciprocity and information distribution (think of the array of recent research on mycelium networks and the 'wood wide web'). The many-stranded forms of research concerned with this many-headed organism form an 'ecological reticulum' (Rheinberger 1997: 182), a network of interconnected concepts and stories which transcend disciplinary boundaries and epistemological systems.

I view my artistic experiments with slime mould as a form of dialogue between empirical, intuitive and explicit knowledge systems, as a means to draw out the biological processes and relate to wider concepts of embodied cognition. My time-lapse studies do not follow the conventions of scientific or natural history filmmaking and they do not present any fixed narrative. Instead, I hope that the visual tropes of time-lapse photography allow the organism to speak on its own terms in a performative way. Through its oscillatory rhythmic flow of cytoplasm,

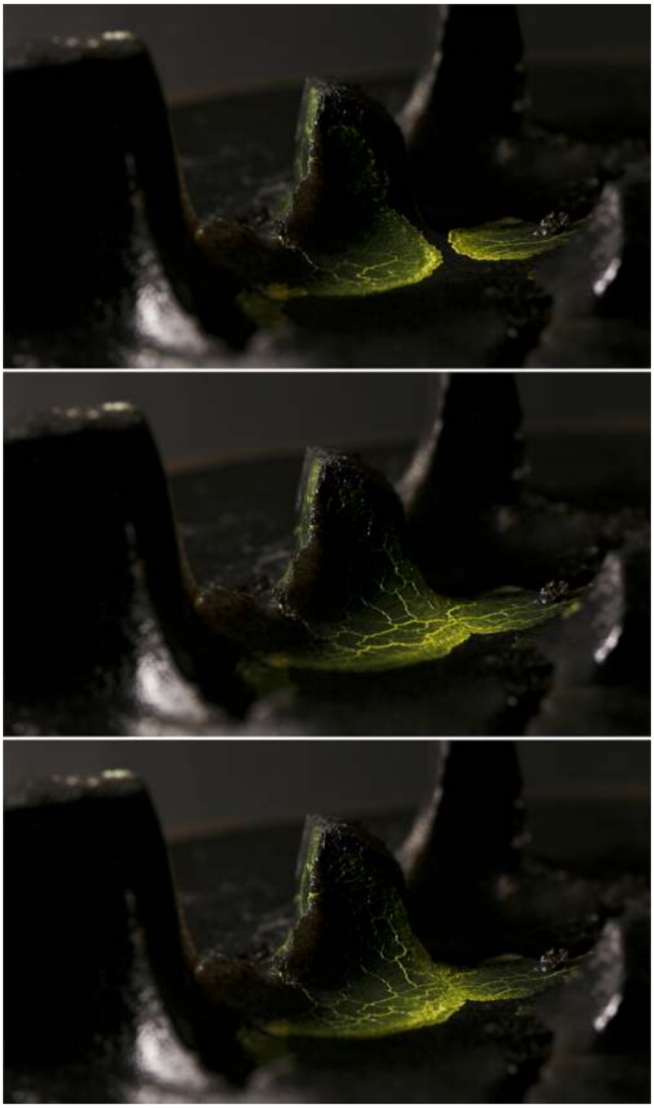

FIGURE 7.9: Film stills from *The Physarum Experiments*, *Study No. 026: Intraspecies Fusion* (2018). © Heather Barnett.

through the constant pushing and pulling of internal forces, the slime mould reveals the 'cognitive' activity of a chemically sensing body, mediated by my interventions.

The titling of the films, a series of numbered 'studies', is purposeful. Used in the domains of both science and art, the 'study' implies a focus on learning through experimentation. A 'study' does not suggest the creation of fully resolved artworks or results, but a mode of enquiry and a state of being in perpetual process. Through the various technical, aesthetic and conceptual choices of experimental design – the level of intervention, shifting cameras positions and ranging interval times – I have built an eclectic portfolio of slime mould studies which are represented and disseminated in different ways (Barnett n.d.b). In addition to being exhibited as artistic works with the usual conventions that apply in that context, the films are also made available online posted on a YouTube channel (Barnett n.d.a). They are listed under a Creative Commons license which grants others non-commercial use of the material. In recent years, *The Physarum Experiments* have been appropriated and integrated into science documentaries, including *Is this slime mould intelligent without a brain?* (Whatson 2019), a gothic opera *Polia & Blastema* (Merhige 2021), an experimental film *Queering Di Teknolojik* (Smith 2019) and a feature-length documentary film about Delhi's air pollution *Invisible Demons* (Jain 2021). As the slime mould aggregates its cellular mass and propagates through its environment, I am curious as to the myriad of interpretations of its behaviours and the attribution of ideas carried (unwittingly) by this curious organism. The slime mould – as a metaphorical and physical body – facilitates the propagation of ideas. In the same way that I cannot control the outcome of my interactions with the organism, I choose not to control how others interpret and represent the organism I have captured on camera.

Relational devices: Drawing out and drawing in

> *Physarum polycephalum offers us something like the degree zero of sentience and of decision-making. Its mode of thinking doesn't involve concepts, or representations, or intentional objects, or self-awareness, or even an underlying unity of experience; it leaves out most of the things that philosophers have traditionally considered to be necessary or intrinsic to thought. And yet, it feels, and ponders, and decides.*
> (Shaviro 2016: 213)

My artistic and intellectual interest in the slime mould is multi-faceted: as a subject, I find it fascinating, as a medium it has inherent aesthetic and behavioural characteristics which can be 'worked with', and as a metaphorical device it relates to many epistemological and ontological concepts. The time-lapse studies, in combination with the other methods of interdisciplinary enquiry I employ, collectively form an experiential and practice-driven 'experimental system'. The films propagate through different contexts and interpretations, they inform workshops and collective experiments, and they help me better understand the inherent properties of the organism itself, with the different elements coalescing and feeding back into each other. Historian of science, Hans-Jörg Rheinberger, defines experimental systems as an assemblage of phenomena, materials, processes and concepts all 'packaged together' (1997: 28). Within the scientific research he critiques, experimental systems operate as 'vehicles for materialising questions, [which] inextricably cogenerate the phenomena or material entities and the concepts they come to embody' (1997: 28). The slime mould embodies a vast number of concepts and phenomena – in literal, material and metaphorical terms. As a collective entity, many cells work cooperatively as a supercell, the organism lends itself to practices of co-generation and co-enquiry. I see my work with slime mould as sympoetic (Haraway 2016; Dempster 2000) – collectively producing – not in a truly collaborative way (clearly the slime mould does not choose to work with me), but in its capacity to embody a multitude of diverse concepts and concerns simultaneously. This assemblage – of organism, material and environmental interactions – can bring together different modes of knowledge, merging the explicit findings of scientific research with the tacit understanding from observation and experience. The staging of the organism, through this assemblage, creates feedback loops between slime mould and environment, between slime mould and human, and between slime mould and itself.

The slime mould, simultaneously one and many, offers a rich philosophical 'discourse object' (Rheinberger 1997), inviting us to speculate … on the nature of self and other, on the identity of the individual and the collective and on the fundamental building blocks of intelligence. Through *looking at* and *looking with* other life forms, I suggest that we might shift our ontological assumptions. As Shaviro argues, 'slime molds allow us to observe the mechanisms of thought in something like their primordial form' (2016: 212) – a mode of thought that is distributed and dynamic, highly attuned to its environmental conditions. Neurons and oscillators alike require feedback loops for decision-making to take place and for any notion of thought to emerge, with elaboration and amplification in the system.

The purpose of the film studies, and indeed of this essay, is to tell visual stories of exceptional single-celled intelligence and invite one species (human) to observe and engage with another (slime mould) with fresh eyes and heightened appreciation. The intention is not merely to depict the slime mould as a biological object of curiosity, but to *draw out* its inherent behaviours as a subject and *draw in* the observer to meet another species halfway (Barad 2007). The work of Anderson-Tempini, Dupré and Wakefield, and the focus of this book, centres on drawing as a process by which we can better conceptualize and visualize the complex processes of life. To *draw* is to represent and make manifest, but it is also to pull towards, to draw closer, to *draw in*. The time-lapse process is intended to mediate between the relative physiological limits of perception and *draw out* that which cannot ordinarily be seen in human time and space. To *draw out* is to entice, to lure something out, to tease into being. A process of gradual extraction, *drawing out* is to prolong, to lengthen the time, implying a pulling of threads or of information (Merriam-Webster n.d.). In human terms, it can mean to induce someone to speak openly, to reveal true feelings. In slime mould terms, it means to amplify processes of life which lie beyond our perceptual grasp and to scale up the organism (literally and metaphorically) in the hope of creating a relational space between two radically different spatiotemporal worlds.

In this chapter, I have explored the processes of life at play within *Physarum polycephalum*. I have introduced different aspects of the multi-faceted scientific enquiry seeking to better understand its fundamental forces and capabilities. I have discussed selected time-lapse studies I have created, working directly with the organism. The intention of this reciprocal interplay – between slime mould and human – is an invitation for an aesthetic pondering on disparate life forces and modes of existence. Whilst we can only 'grasp the slime mold's experience partially and indirectly, by its actual behavior and by the traces of evidence that it leaves behind' (Shaviro 2016: 215), the temporal amplification offered by technological mediation permits access to some tacit understanding of the modes of decision making which occur within the organism as it operates in constant dialogue with its Umwelt. This relational encounter may encourage us to challenge our own definitions of intelligence, where human-centric (and therefore neuronally biased) positions are called into question by an embodied and chemically sensitive form of knowing. But this is not purely an altruistic exercise in ontological speculation. If humans can contemplate the subjective experience of the slime mould perhaps, we can, in turn, reflect on our own sensorial world and think about how decisions are made in dialogue with our own environment.

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8

Mimicry, Adaptation, Expression

Wahida Khandker

The Comma butterfly (*Polygonia c-album*) is normally a conspicuous sight, its wings, when open, being scallop-edged, a muted orange colour and flecked with dark spots. Apparently spending most of its short adult life (in total, ten to twelve months) in winter hibernation, the Comma is also able to evade predators during 'wintering' thanks to the colouring of the underside of its wings (save a small, white comma-shaped marking, for which it is named), that bear a remarkable resemblance to dead leaves (Wiklund and Tullberg 2004: 621). Orchids are also notable for their 'deceptive' properties in their case used to achieve pollination. A slipper orchid (*Cypripedium subtropicum*) has dark brown flowers, with tufts of short white hairs, and its odour is that of rotting fruit. The white tufts have all the appearance of an aphid colonization of the flower, and this attracts hoverflies to feed on them. Whilst only aphid-like in appearance, the tufts are in fact still edible, enough to entrap the feeding hoverfly that easily falls into the orchid's 'slipper' or pouch. The struggle to exit the pouch requires that the hoverfly brushes against one of the flower's anthers, and the insect escapes with a generous dusting of pollen to carry to the next plant.[1]

Mimicry is an extraordinarily common natural phenomenon and emerges with varying and surprising complexity across both animal and plant kingdoms. This chapter examines evolutionary and ethological instances and concepts of mimicry in response to Gemma Anderson-Tempini's 'Isomorphology' project and its development into artworks and methodologies that she names 'Isomorphogenesis'. The first section considers the concept of mimicry as described by Henry Walter Bates, a contemporary and correspondent of Charles Darwin and Alfred Russel Wallace, and how definitions of mimicry have since proliferated to try to match its complex variations in the natural world.

I will turn in the second half of the chapter to the dynamics of camouflage and mimicry in cephalopods. Peter Godfrey-Smith's book, *Other Minds: The Octopus and the Evolution of Intelligent Life* (2017), has done much to popularize interest in cephalopod consciousness, as an effective way of 'making strange' the idea of mind, the study of which has hitherto tended to be determined by the 'ideal' of human consciousness. Even so, in places, Godfrey-Smith's study tends towards that exceptionalism when he compares the complexity of cuttlefish signalling with that of a group of baboons. In both, he writes, he cannot help seeing 'an unfinished quality. […] On the cephalopod side, there's a simpler social life, hence less to say, but such extraordinary things expressed nonetheless' (Godfrey-Smith 2017: 133). In this chapter, my aim is less to find the purpose or recipients of such 'messages', as evidence of social complexity, than it is to highlight the dynamics of interaction between animals and their environments liberated from more teleological determinations of them. The processes of drawing seem to lend themselves more to this alternative focus. In drawing, it is the body that orients itself in complex ways to its surroundings and allows for duplication or mimicry. It does not require an audience or a recipient of messages. It requires instead an intensity of concentration comparable to that involved in philosophical study. In the final section of this chapter, I compare the movements of cephalopod colour changes to the processes involved in the activity of drawing. Whilst there is a descriptive language that we can borrow from scientific studies of cephalopods that might illuminate the at once mimetic, adaptive, and expressive qualities of drawing, I will propose, conversely, a reading of cephalopod 'artistry' in the light of Isomorphogenesis, as an alternative means of thinking about the dynamics of cephalopod rapid camouflage and perhaps also about multi-species interactions within their broader ecosystems.

Iterations

Modern scientific discussions of the evolution of mimicry recall the observations of Henry Walter Bates, in his pithily-titled 1862 paper, 'Contributions to an Insect Fauna of the Amazon Valley. Lepidoptera: Heliconidae'.[2] His study focuses on the co-existence of mimetic species with their mimicked counterparts (later in the scientific literature referred to as 'models'), whilst the selecting agent will usually be a predatory insect or bird. Bates speculates that the presence of such mimicry indicates how nature is '*striving* after a correct imitation' (Bates 1862: 505). Indeed, this striving is not only found in the Lepidoptera, he continues, but across many orders of insects, such as parasitic bees and two-winged flies which 'mimic in dress various industrious or nest-building Bees, at whose expense they live in the manner of the Cuckoo' (Bates 1862: 506).

Bates refers to Darwinian natural selection as the most convincing explanation of the emergence of such mimics (Bates 1862: 511–12), as opposed to evolution in a definite direction or the inheritance of acquired characteristics (Lamarckism). One explanation is that butterflies which appear to mimic one another evolve separately and only converge incidentally. However, Bates proposes that mimics do seem to adapt to their models, and they persist because such a 'strategy' benefits both, with their would-be predators concentrated on devouring the many other varieties in the region instead (the Heliconid models' form is successful in signalling their unpalatability whilst their mimics, in their resemblance to them, benefit without eroding the effectiveness of the unpalatable 'branding'). Bates's study features illustrations of instances of mimicry by 'palatable' species, *Leptalis*. The top row of images of this particular species, for example, shows its 'normal form' with broader white wings, flanked by its slender-winged and colourful variations. Their mimicry was thought to be modelled on the more 'unpalatable' species such as *Ithomia* (which Bates illustrates below the set of mimics). The naturalist uses the presentation of such images to illustrate the 'origination of a mimetic species through variation and natural selection' (Bates 1862: 564). *Leptalis*, Bates continues, even displays in a range of existing varieties 'the process in different stages of completion' (Bates 1862: 565). He justifies this particular mechanism of mimicry between butterfly species, in opposition to mere convergence in response to shared physical conditions, by comparing them with the mimicry of inanimate objects. Instances of mimicry between living beings are

> phenomena of precisely the same nature as those in which insects and other beings are assimilated in superficial appearance to the vegetable or inorganic substance on which, or amongst which, they live. The likeness of a Beetle or a Lizard to the bark of the tree on which it crawls cannot be explained as an identical result produced by a common cause acting on the tree and the animal.
>
> (Bates 1862: 508)

A review of the subsequent literature on mimicry shows an emphasis on efforts to classify the plethora of modes of 'disguise'. This might be in terms of combinations of colour, texture, and scent in multiple species and as 'enacted' by some species that are capable of changing their appearance (typically, reptiles, cephalopods, etc.). *Batesism* is reserved for palatable species that mimic nearby unpalatable ones, as detailed in Bates's initial study. *Crypsis*, on the other hand, describes the phenomenon of camouflage, the effect of which is to be completely hidden from potential predators or prey. *Masquerade* refers to the instances of resemblance between an animal and parts of plants or inorganic materials (Endler 1981: 29). Our Comma butterfly, in its resemblance to a dead leaf, fits into the latter category. These classifications expand even further to try to distinguish them from the broadest concept of the repetition of likenesses: *Convergence* in which resemblances arise amongst otherwise distinct species. What *unites* the different classes of mimicry is their basis in a three-part signalling system involving a mimic, its model and an operator or 'receiver' (e.g. a predator). The successful mimic achieves resemblance to its model, to a sufficient degree to fool the receiver. One interesting aspect of discussions of such 'mimetic' signalling systems is the acknowledgement that only an *imperfect degree* of mimesis, for example a mere split-second glance of colour and shape by a predator that might seem wholly unconvincing to the human eye (and its accompanying expectations), is required to fool one's audience. Stoddard (2012) proposes the use of 'quantitative models of avian colour, luminance, and pattern vision' to supply a 'birds eye view' of different examples of mimicry (Stoddard 2012: 630). What, in other words, might birds actually see when seeking out their prey? Stoddard notes that 'mimicry rings have been characterized from the human visual perspective, but this can be dangerous given that avian predators may have different perceptual biases' (Stoddard 2012: 639). That is, the standard of similarities that the human eye might require to be deceived may well be quite different to that required by a bird on the hunt for its prey.

Thinking in terms of signalling systems in the study of intraspecific and interspecific communication amongst non-human animals invites comparison, if often only negatively, with human forms of communication. The definition of language, understood as a system of communication according to specific rules (syntax, grammar, etc.), serves as an insurmountable obstacle to drawing affinities between human and nonhuman animals. Daniel Heller-Roazen resists such inevitable conclusions in *Echolalias: On the Forgetting of Language* (2005). The distantly imitative babbles of a child learning to speak are not simply lost or transcended in the entry into 'real' language, but rather persist. They do so in *onomatopoeias* that seem to 'represent the last remnants of an otherwise-forgotten babble or the first signs of a language still to come' (Heller-Roazen 2005: 14). Elaborating further on the cross-cultural recurrence of onomatopoeic sounds in both child and adult speech, he notes some common examples in English:

> take the 'apico-alveolar' or 'rolled' *r* that Anglophone children once used in imitating the sound of a ringing telephone; or the 'dorso-velar' or 'trilled' *r* often produced to mimic the purring of a cat, which strikingly recalls the liquid consonants in modern French and German.
>
> (Heller-Roazen 2005: 16)

Language, it is claimed here, is 'never more itself' than when it is straying across its perceived boundaries into other languages and across the threshold of the animate into the inanimate (Heller-Roazen 2005: 18).

Human capacities in general might be characterized, in contrast with other animals, by failure or 'doing less' (Heller-Roazen 2005: 131). The virtue of failure, or the paradoxical status it possesses, is one that we might see similarly in language acquisition. Heller-Roazen finds its expression in an aphorism of Franz Kafka, in which he muses that he 'can swim just like the others', but having a better memory, he has also not forgotten his *in*ability to swim: 'since I have not forgotten it, being able to swim is of no help to me; and so, after all, I cannot swim' (Kafka, cited in Heller-Roazen 2005: 146).

The forgotten (inactive) is interlaced with the present (active) language in one more literary example of interest.[3] A young man takes lessons in the Persian language from a non-native speaker of it, and he goes on to compose what he thinks are some superlative pieces of poetry in his newly learned tongue. In the end, he finds that what he had been taught was not, in fact, Persian at all, but such a badly remembered facsimile of it that it is incomprehensible to everyone except the budding poet. 'But can one be sure?', asks Heller-Roazen, 'Perhaps it is not the master but the student who forgot the language and, in complete isolation after the departure of his teacher, gradually developed an idiom of his own that hardly resembled the one he had been taught' (Heller-Roazen 2005: 200). In such instances, Heller-Roazen's analysis of the significant role of improvisation, error and 'unlearning' echoes Henri Bergson's distinction between instinct and intuition in his 1907 work, *Creative Evolution*. Bergson observes a key difference between human intelligence and the relative perfection of an insect's instinctive actions. He cites the complexity of actions of various species of Hymenoptera (e.g. bees and wasps). 'The yellow-winged Sphex', Bergson writes of this small wasp,

> which has chosen the cricket for its victim, knows that the cricket has three nerve-centres which serve its three pairs of legs – or at least it acts as if it knew this. It stings the insect first under the neck, then behind the prothorax, and then where the thorax joins the abdomen.
>
> (Bergson 1998: 172)

From the perspective of the entomologist, one would suppose that a thorough survey of the anatomy and physiology of the species of cricket would be required for such knowledge, given the procedure of human intelligence that typically reduces the parts of the organism to a concept or 'external' knowledge of its whole. The wasp, on the other hand, seems to operate with something more akin to a *sympathy* (meant, writes Bergson, in its etymological sense) between the two insects, 'considered no longer as two organisms, but as two activities' that exist in an internal or fundamental relation to one another (Bergson 1998: 174). The possibility is open to human intelligence to *forget* or to *unlearn* its own habits, concepts, and expectations that frame its day-to-day experiences. It is possible to achieve something akin to the wasp's sympathetic relation in what Bergson refers to as intuition, which would be a form of instinct that could 'become disinterested, self-conscious, capable of reflecting upon its object and of enlarging it indefinitely' (Bergson 1998: 176).

In the next section, I turn to Gemma Anderson-Tempini's 'Isomorphology'[4] method that in some ways responds to Bergson's call for analyses that are grounded in sympathy or alignment with living processes, in a certain anti-reductive perspective on the persistence and repetition of forms. This approach will also resonate with Chiara Ambrosio's chapter in this volume, in which she explores the integral role of drawing in the philosophical practice of pragmatist philosopher, Charles Sanders Peirce. Whilst the broad association between Bergson and pragmatism, through his exchanges with William James, already invite some comparisons between these philosophical approaches that seek to reinvigorate our ability to connect with living processes, Ambrosio's study of the possibilities of Peirce's 'pragmatist visual epistemology' adds a compelling dimension to this endeavour.

Isomorphology

Gemma Anderson-Tempini cites key works by Michel Foucault and John Dupré in which both thinkers offer critical perspectives on the practices of classification within the life sciences. In *The Order of Things*, Foucault considers the historical treatment of the growth of the life sciences in the eighteenth century. The particular aim of the more conventional historical interpretation, he notes, is to illuminate the transition to an analysis of living things that might have prepared the way for Darwinian evolutionism. Foucault sees, on the other hand, not an increased curiosity about life in that era nor the consolidation of acquired knowledge, 'providing a ground for the more or less irregular, more or less rapid, progress of rationality' (Foucault 1973: 158). Rather, natural history in the eighteenth century, not yet the science of biology that we might recognize now, involved a re-organization of visible elements. For example, Foucault notes a tendency in sixteenth-century studies of plants and animals to identify them by 'the positive mark', such as the tendency of one species of bird to hunt at night, as opposed to another that feeds on carrion (Foucault 1973: 144). He contrasts this with the seventeenth-century classification that attempts to organize species in a table of identities and differences. Cuvier's ordering of the animal kingdom into four divisions (Vertebrata, Mollusca, Articulata and Radiata[5]) sets the scene for an approach to classification that reduces species to their relative adherence to certain laws or unities of the organism ('skeleton, respiration, circulation')

(Foucault 1973: 145). The age of botanical and zoological gardens was only preceded, historically, by other presentations of animals as spectacle (e.g., in fairs and tournaments). Thus, Foucault argues, ‘what came surreptitiously into being between the age of the theatre and that of the catalogue was not the desire for knowledge, but a new way of connecting things both to the eye and to discourse’ (Foucault 1973: 131).

John Dupré’s book, *The Disorder of Things* (1993), proposes a *radical ontological pluralism* in which objects can be classified in numerous objectively grounded ways that may serve a variety of purposes and perspectives that make up the biological sciences, enmeshed as they are in a range of complex and changing human practices. Dupré identifies a number of problems inherent in the search for the unification of the sciences, a project built upon essentialist, reductionist and determinist principles. For example, an assumption that there might be natural kinds, or ‘a class of objects defined by common possession of some theoretically important property’ (Dupré 1993: 22), in biology that can be used to verify their extension in everyday language, proves to be problematic. Rabbits and hares whilst belonging to the same genus, *Lepus*, are quite distinct in cultural terms that do not essentially make sense in biological terms (Dupré 1993: 29). In the context of ecology, the study of the dynamics of interacting populations, we might be interested in either rabbits or hares as the typical prey of lynxes, but it is not the case that the ideal properties of each of these three ‘kinds’ (at a ‘microlevel’) would usefully inform the study of the overall interacting populations (at a ‘macrolevel’) (Dupré 1993: 118–19). Dupré also points to the importance of molecular genetics in the reinforcement of reductionism as a marker of legitimacy in the biological sciences. The movement between levels, so defined in the specific terms of each scientific field, is evidently informative, but the ultimate reduction of them all to, say, genetics, does not necessarily always yield useful predictions. Rather, the interactions of all of these levels, within evolutionary and ecological *processes*, allow for more productive insights into living populations. To return to Dupré’s overarching argument, ‘there are genuinely causal entities at many different levels of organization. And this is enough to show that causal completeness at one particular level is wholly incredible’ (Dupré 1993: 101).

In the spirit of both Foucault’s analysis of the reorganization of visible elements in the construction of classificatory systems and the malleability of classificatory descriptions promoted by Dupré, Anderson-Tempini explores the heterogeneity of the species concept. Its demarcations are predicated on a multiplicity of shared features across organisms, in a new visually oriented, rather than linguistic, classificatory system, and it is one that does not seek to delineate resemblances between only living organisms but also between animal, vegetable and mineral forms (Anderson-Tempini 2019: 78). The resulting system is a series of abstract forms that represent tendencies towards, for example, bilateral and three-(or more) fold symmetry, branching, or spirals (Anderson-Tempini 2017: 79, Figure 8).

We can, of course, think of the stages of Anderson-Tempini's method as an accentuation of drawing as a kind of mimicry, not simply in the familiar (historical, philosophical, aesthetic) sense of 'mimesis', but more especially in a sense that is readily comparable to the biological examples I have discussed so far. It can also be said to extend the 'project' of evolution itself in its imperfect repetitions of forms across individuals and generations of organisms. Anderson-Tempini herself highlights the comparison with organic development in her method, not least insofar as drawing is, Anderson-Tempini explains, a 'dynamic sensory transference from the optic to the kinaesthetic to the haptic that requires concentration and interactive decision-making' (Anderson-Tempini 2019: 18). Below, I provide a brief outline of some of the methodological elements central to the classificatory studies of Isomorphology. It provides the foundation for Anderson-Tempini's later work on 'Isomorphogenesis' that, as I indicate in the final section of this chapter, culminates in Anderson-Tempini's collaborative project with Wakefield and Dupré on 'Drawing the Dynamic Nature of Cell Division' featured in the present volume. We will see, over the following sections, how the idea of mimicry is given expression and transformed from the iteration of familiar forms to the reconceptualization of energy fluctuations that is both familiar and pushes the research in this field to its bounds, such that it might generate new knowledge.

In the first stages, observation, perspective, decision-making and classification, several specimens are selected and matched against a form in the Isomorphology system (e.g. bilateral symmetry in a butterfly, a leaf, a beetle), and an etching of each is immediately made onto a copper plate. Anderson-Tempini remarks on the immediacy of this process, which opposes the traditional view of 'sketches' as preparations for a final work. The sketches are not discarded in this case, but instead comprise the final work. Drawing, then, develops and adapts, in much the same way as a living organism's own processes do (Anderson-Tempini 2019: 98). The immediacy of this copper 'sketch' perhaps belies the complexity of the process of drawing involved. As Anderson-Tempini explains, observational drawing involves 'hand-eye coordination, analysis, delineation, abstraction, improvisation, collage and deep concentration' (Anderson-Tempini 2019: 94). Each act of drawing is not simply the sweep of a hand, forgotten and overwritten by the next, but a process of learning how the parts of an object coalesce. The adoption of a particular perspective on the specimen necessarily obscures another, accentuating this as deliberate *selection* rather than a 'pure perception' of the object.[6] It is an accumulation of knowledge as deliberate and intricate as the study of a philosophical text can yield, and yet, like any reading of a text, it results in an imperfect replica that, if one is open to it, can lead to new insight.

The next stages of translation, abstraction and improvisation speak to this openness to the creative possibilities of the drawing process. The aim here is not *accuracy*, the achievement of which we have already seen could only align with a view of scientific observation as purely 'objective'. Establishing the set of symbols in the system of Isomorphology involved the translation of observed similarities into two-dimensional symbols. The processes of selection and composition subsequently require the observer to project the two-dimensional symbols back onto real objects (Anderson-Tempini 2019: 95). The act of 'abstraction' is not intended as a perfection or reduction of things to an ideal, but rather as the beginning of a process of 'unlearning' the conventions of classification[7] (Anderson-Tempini 2019: 96). Finally, the openness to 'improvisation' is necessitated by the immediacy of drawing onto copper plate, and the willingness to commit to each line and to work out any problems in the available drawing space (Anderson-Tempini 2019: 96). Anderson-Tempini also points here to the physical orientation required, best described in the way in which 'the trace of a walk can be compared to the trace of a drawing: a body scaling the landscape as the hand and drawing tool scale the page, or as Klee famously put it, 'taking a line for a walk' (in Anderson-Tempini 2019: 22).[8]

In the next section, I proceed with a description of the behaviour and anatomical features of cephalopods that enable their camouflaging ability. There, I want to incorporate some of Gemma Anderson-Tempini's reflections on her evolving observational drawing practices, as a way of thinking a little differently about cephalopod biology.

One of these things is not like the others

Predating the evolution of vertebrates, the earliest cephalopods are thought to have evolved around 530 million years ago (Hanlon and Messenger 2018: 7). This special group of molluscs includes animals such as the soft-bodied cuttlefish, squid and octopus. Displaying a high visual acuity, which allows them to study their surroundings in great detail, they are then able to translate what they see around them into numerous 'matching' bodily orientations (chromatic, locomotor, etc.) with great rapidity. Their hard external-shelled relative, the nautilus, resides in deeper waters, whilst the shallow water dwellers evolved alongside fish and, it is observed, they seem to be 'more fish-like than molluscan' in their behaviour (Hanlon and Messenger 2018: 9). Their complex behaviour, in particular their responsive use of body patterns and colour changes for either camouflage or display, reflects their highly developed nervous systems (as discussed, in terms of features of consciousness, in Godfrey-Smith's work) and more readily enables comparison with what we traditionally think of as 'higher animals'.

First, consider the mechanisms of cephalopod skin texture and colour changes. In mammals, the organs with which we respond to stimuli, our 'effectors', are our muscles, whereas in cephalopods, their bodies incorporate a system of 'effectors' such as chromatophores, reflecting cells, an ink sac, a beak, as well as their arms and suckers. The chromatophore organ, basically a pigmented cell surrounded by a set of radial muscles under direct neural control, which is central to their camouflaging ability, is quite distinct from those present in the skin of crustaceans, amphibians and reptiles.[9] Their natural pigmentation includes black, brown, red, orange and yellow. They are thought to emit blue, green and violet through 'structural' means only (comparable perhaps to the blue hue arising from the structure of bird feathers, such as those of the jay), or from the use of reflecting cells, iridiphores and leucophores (akin to the cooler hues of magpie feathers). Interestingly, cephalopods are believed to be colour blind, so mimicry of their surroundings is thought to concentrate on shade and texture, whilst their reflecting cells allow for more accurate 'colour-matching' (Hanlon and Messenger 2018: 36–38). Contraction of the chromatophore creates a lighter colour on the skin surface (because it exposes the lighter reflector cells), whilst the expansion of the chromatophore darkens the skin. Critically, the neural control of chromatophores allows for the animal to change the appearance of different parts of the skin at the same time, thus enabling them to create complex 'images'.

Hanlon and Messenger go on to break down the organization and structure of body patterns (the collection of textural, postural, locomotor and chromatic changes) of cephalopods into units and components that, together, add up to the total appearances of the animal at any given moment (Hanlon and Messenger 2018: 53; Messenger 2001: 514). However, for our purposes, the precise demarcation of such elements is less significant than the processes in which they participate. They discuss the significance of 'edge detection' or 'edge perception' as a particular feature of the visual acuity of cephalopods, one that is comparable to vertebrates (including humans). Further research on the dynamics of camouflaging in cuttlefish also indicate their reliance on visual cues, such as 'spatial scale, background intensity, background contrast, object edges, object contrast polarity, and object depth' (Hanlon and Messenger 2018: 67).

Recall now Anderson-Tempini's system of abstract forms. Whilst cephalopod bodies may themselves be seen as echoes of the different forms of symmetry, a number of elements of the cephalopod research cited above tend towards the observations of Goethe and Klee who, as Anderson-Tempini writes, 'both realized that only by penetrating to the smaller units, which made up the complex composite plant, could the inner dynamics of nature be confronted' (Anderson-Tempini 2019: 138). The possibilities available to the cephalopod to alter its appearance, through its contracting-expanding chromatophores, for example, suggest that their pattern-production might be articulated using Klee's colour gradation technique that interprets the gradations of colour 'synaesthetically' in terms of a musical scale:

> Klee also used the musical terms major and minor to describe types of contrast ('direct major contrast/indirect major contrast') – implying that he considered scale as structural articulations of the movement of natural form. […] For Klee, colour gradation also has an emotional charge and tension; he talked of the character and movement as varying from a quiet rise and fall to an open struggle, characteristics also evident in biological movement.
>
> (Anderson-Tempini 2019: 145)

We saw in the discussion of Bates's butterflies, how mimicry is now variously sub-categorized according to the effects on the 'receiver' of the visual signals of the mimic. Researchers on this phenomenon in cephalopods categorize their body patterns into three basic pattern 'templates': Uniform (a high resolution pattern, so to speak), Mottle (medium resolution) and Disruptive (high contrast shapes). The latter comprises 'distractive marking', itself broken down into the appearance on the body of a White Head Bar, a White Triangle and/or a White Square (Hanlon and Messenger 2018: 101–03). The effect of these rather conspicuous markings is to confuse or *disrupt* the visible outline of the animal, enabling it to sit amongst a pile of rocks or other marine debris and to be lost amongst the general disarray of the scene. These modes are deemed to be defensive forms of 'crypsis' since they serve as an *absence* of any signal. The interpreted aim, it seems, is to fool the potential predator that 'there is nothing to see here'. Take, in addition, the example of 'countershading' which involves 'the elimination of any silhouette or shadow created by downwelling light' (Hanlon and Messenger 2018: 107). In this mode, 'the dorsal chromatophores are expanded' (that is, the upper side of the animal is darkened), 'the ventral chromatophores are retracted' (its underside is lightened) and 'those along the side of the mantle and arms are beautifully graded between the two extremes' (Hanlon and Messenger 2018: 107).

Accompanying all such categorizations of 'behaviour' is the acknowledgement of their limitations. One such limitation of the 'bio-semiotic' characterization of mimicry seems evident in the unending variety of complex postures adopted by cephalopods with the ever-increasing sub-categorizations invented to attempt to account for them (and, indeed, we can see this 'arms race' between subject species and their human observers in the scientific literature on mimicry in general).[10] Recall, for example, the category of 'masquerade', in which animals resemble parts of plants or inanimate objects. Masquerade is deemed adequate to describe the display of the underside of the wings of the Comma butterfly, which only requires it to close its wings and to sit still. It is also deemed equally adequate to describe the complex neural manoeuvres of posture, skin texture and colour enacted by 'the tiny sepiolids *Idiosepius pygmaeus* [that] attach themselves to the underside of a seagrass blade with a dorsal adhesive organ to mask their body form' and that 'sometimes drift in a head-down posture and resemble floating algae, seagrasses and flotsam' (Hanlon and Messenger 2018: 113). Other complex, and more 'inventive' actions are noted under the heading of 'Protean behaviour', again defined in terms of the effect on a pursuing predator. The 'Blanch-Ink-Jet manoeuvre', as the name indicates, describes a cephalopod turning a pale colour, ejecting ink and jetting away, only to leave an ink blob in its place (Hanlon and Messenger 2018: 129). Then, as if to up the ante, an intriguing observation follows, referring to 'small *Sepioteuthis sepioidea* high in the water column on coral reefs ejecting small blobs of ink, then turning all dark themselves and hovering amidst the blobs in some sort of imitation or general resemblance to the ink' (Hanlon and Messenger 2018: 130). Such examples would suggest that there is more in common between cephalopod mimicry and that of songbirds, insofar as it involves a much more immediate set of interactions and 'improvisations' between the animal and its surroundings. In an analysis of post-Batesian attempts to define biological mimicry, Wickler (2013) in fact cautions *against* the application of categories of (evolutionary) biological mimicry to explain forms of 'cultural' or 'social' mimicry (acquired characteristics), such as birdsong, as straying dangerously from Darwinian into Lamarckian territory. He provides examples of mimicry in birdsong, such as the satin bowerbird's replication of the 'laugh' of a kookaburra, to illustrate the flaws in extending the same categorization of visual and structural forms of mimicry to vocal forms (Wickler 2013: 265). However, a productive comparison may yet be possible between the rapid camouflage of cephalopods and the inventive song compositions of birds. Even if vocal mimicry is read as a means of attracting attention in the 'soundscape' of the forest ecosystem, and cephalopod mimicry is primarily 'cryptic' in the light of shallow waters, *both* indicate the capacity for complex interactions with, and interpretations of, their environments beyond mere instinctive 'behaviours'.

What might result if we rethink cephalopod (and, indeed, other species) interactions in terms of Anderson-Tempini's drawing method? There, a drawing is not just a signal, a meaning to be communicated. It is also both a deeply contemplative and, at times, spontaneous activity. There is already a resonance between the activity of the artist and that of the keenly observant cephalopod (recall the process of drawing involving 'hand-eye coordination, analysis, delineation, abstraction, improvisation, collage and deep concentration' [Anderson-Tempini 2019: 94]). Marine biologist, Roger Hanlon, cites his recent work with art students and practitioners, noting that 'artists are particularly adept at pattern and edge design, which are key features in animal camouflage and signalling. Artists are trained to recognize and manipulate these design features and incorporate them often in their products'.[11] Anderson-Tempini's development of the Isomorphogenesis project suggests a unique perspective here, as I will outline in the next section.

Isomorphogenesis

Gemma Anderson-Tempini writes of her collaboration with mathematician, Alessio Corti, on drawing four-dimensional trees, that it demonstrated 'the possibility of creating work from a kind of drawing algorithm involving drawing actions (verbs) performed on a set of primitive shapes rather than from observation' (Anderson-Tempini 2019: 176). This is explored further through her participation, as she recalls, in the 2013 'Evolutionary Drawing' workshop, looking at the manipulation of primitive forms through 'FormSynth' drawing rules. Anderson-Tempini's adaptation of this system centres on the identification of a set of parameters or characteristic features, and an algorithm or 'sequence of unambiguous instructions for carrying out the procedure of drawing' (Anderson-Tempini 2019: 185). Added to these principles for drawing are those from 'Theoretical Morphology' which explores existing forms within a theoretical space, as a subset of its possible forms: 'instead of isolated sketches of non-existent forms (Cyclops, Dragons, Centaurs, etc.) the non-existent forms of theoretical morphology occur in a smooth continuum of transitional forms that range from existent to non-existent in a morphospace' (correspondence with McGhee, cited in Anderson-Tempini 2019: 188).

Looking at the Isomorphogenesis series of drawings suggests, to me, that Anderson-Tempini's method lends itself to the exploration of cephalopod rapid camouflage. As we have seen, research already suggests that the cephalopod's repertoire of body patterns is limited to certain grounding forms (e.g., Uniform, Mottle, and Disruptive, discussed above, as well as the examples of 'countershading' and Protean behaviour). That is, we have a specific sequence of actions in accordance with 'rules' akin to an artists' visual repertoire. The system of chromatophores and reflecting cells serve to limit the parameters of colour-change at a structural level. Indeed, a paper by Yu et al. (2014) outlines the adaptation of such principles in the development of artificial camouflage in the form of a thin textile sheet mimicking different layers of cephalopod skin: 'chromatophores' containing thermochromic dye (to enable colour to change with temperature), layered over silver, chosen for its light-reflective properties (Yu et al. 2014: 13000). This attempt at mimicry of the cephalopod's camouflaging ability is necessarily constrained by its instantiation in artificial materials, but it also points to the possibilities provided by inorganic materials to visualize purely theoretical configurations of their organic models (in this case cephalopod skin).

Could Isomorphogenesis incorporate cephalopod skin 'verbs' within a drawing space, not simply to replicate it (as the 'camouflaging textile' does), but as an expansion of the Isomorphogenesis method? The use of 'verbs' in the context of this later development of Anderson-Tempini's work is less concerned with a direct 'translation' (which, as we have already seen, was already subject to creative improvisation in the method of Isomorphology) than with exploring the limits of visual expression. That is, in order to select verbs that somehow reflect the fluctuating energy patterns of a cephalopod's skin, it is necessary to think of each change not as reducible to, or an attribute of, some particular emotion (e.g. aggression, fear, curiosity, and so on), but rather to view each fluctuation as an expression that affirms only its own 'energy'.[12] In Anderson-Tempini et al.'s mitosis chapter, the progression across Drawing Labs 2 and 3 involves imagining the process of mitosis from the more traditional five or six steps up to a less conventional fifteen stages that might invite the sense of a continuous process. Thus, in our envisioning of the emotional fluctuations signalled by the cephalopod's skin, relevant verbs would need only signal 'energetic' changes in orientations of drawing, such as 'scatter' (using dots), or 'compress' (to instruct the condensation of a set of lines), or 'condense' (to intensify a wash of colour).

Could this, then, be a way to explore what it means to see the world through cephalopod bodies, in their unique morphospace, as a further liberation from direct (human) observation? Take some other examples of cephalopod body patterning, such as the high-contrast striations of 'Intense Zebra', that appears to be a 'confrontational' display, typically between two males. Other studies refer to the hypnotic waves of 'Passing Clouds', the purpose or meaning of which remains far from obvious. In earlier studies, this was referred to as 'wandering clouds'. Evocative of William Wordworth's poem, this display involves the motion of alternating dark and pale waves of colour across the body of the cephalopod. Messenger (2001: 485) cites it as a nineteenth-century appellation, and other researchers attribute it to F. B. Hofman's identification of *Wolkenwandern* (see e.g. Hofmann 1907), typically as a response to trauma or even as a residual response *post mortem*.[13] Encouragingly, the less intrusive development of research in the field provides evidence of Passing Cloud as a common cephalopod display in their natural habitats, and Hanlon's recent studies of the flamboyant cuttlefish show a more complicated 'Flamboyant Display' involving a combination of Passing Clouds, with yellow, red, white and brown coloured markings across the body (Hanlon and MacManus 2020: 2). How might we envisage the sensorial rules that govern Intense Zebra and Passing Clouds? What drawings might this yield in 'Isomorphogenetic' space? A cephalopod algorithm could be explored in this method, and it might help us to envision its sensory-expressive morphospace, commencing with basic forms and radiating outwards into different parts of the morphogenetic landscape, in the direction of specific instances of mimicry or towards more free-form expression in colour, shade and shape. Indeed, this could be expanded even farther across species and sensory boundaries, to the construction of morphospaces for different ecosystems. The integration into Isomorphogenesis of the principle of Klee's synaesthetic colour gradations, at once visual and aural, indicates the possibility of visualizing forms expressive of the avian soundscape, the rhythms of bat echolocation, or the drifting patterns of the territories of large roaming predators, such as wolves or polar bears.

My speculations here, on the possible application of Isomorphogenesis to a broader spectrum of living processes, towards a more abstract 'sensory-expressive morphospace', seek, then, to expand upon Anderson-Tempini, Dupré and Wakefield's work in the present volume. As we saw earlier, the use of drawing verbs is not simply a translation from one language (each stage of the process, as the scientist might describe) to another (a representation, or mimic, in visual form of the scientist's description). Rather, the verbs enable the scientific concepts, or the familiar concrete descriptions, to become 'disoriented', so to speak and to lose their familiarity.[14] The utilization of verbs (invested only with their own expressive force) allows the iterative development of drawings to push the more familiar language, or structure, to its limits. The process of mitosis, as observed by Anderson-Tempini et al., tends to be 'translated' for us into measurable elements through the increasingly sensitive lenses of modern microscopes, such that cell biologists have less agency and imaginative investment in the images they study. The subsequent development of drawing verbs that aim specifically to communicate more abstract processes underpinning each stage of mitosis start to stray from resemblance of forms or stages, to a more imaginative visualization of the amounts or intensities of energy required to enact different (adjacent) 'possibles'. The final set of images of mitosis 'pots within pots' is extremely abstract, and yet succeeds in creating a unique visual vocabulary to communicate energy fluctuations. It remains a kind of mimicry, but one that now features 'imperfectly remembered' forms and processes, and it is therefore able to generate discussion rather than to delimit or to conclude it.

John Dupré's call for a radical ontological pluralism in the sciences summarizes two key aspects of Gemma Anderson-Tempini's work in the move from Isomorphology to Isomorphogenesis: first, pluralism and the relevance of forms across levels and disciplines and, second, the ontological priority of process, in which divergence in a series allows for the emergence of novelty whilst ensuring consistency and the biological integrity of an organism or a population. I have situated Anderson-Tempini's method and artworks within an evolutionary context of the impulse towards mimicry in natural forms, both animate and inanimate. The visual vocabulary of Isomorphology shows an appreciation of such reiterations across nature whilst also incorporating a certain tendency towards imperfectly remembered forms in the improvisational stages of the artist's method, echoing the central role of mutation in the processes of natural selection, as well as the processes involved in philosophical writing (at least in the case of the present chapter). This method is developed further in Isomorphogenesis, notable for its surrendering of agency to algorithms in order to explore inorganic interventions into organic formations. Together these creative methods reflect an interest in representation and repetition (mimicry) but also in exploration and expression. In our age of imperilled species, the ambition to see and to appreciate the natural world through multiple, and more-than-human, perspectives, feels especially timely.

NOTES

1. See Jiang et al. (2020: 1216), for a study of this orchid (mimic) – aphid (model) – hoverfly (receiver) system that includes both visual and chemical mimicry to attract and 'reward' the receiver.
2. A selection of Bates's correspondence with Darwin, which commenced in 1862 and continued until Darwin's death in 1882, can be found in Stecher (1969).
3. From Italian writer Tommaso Landolfi.
4. In Anderson-Tempini (2019), the 'Isomorphology' project is defined by its use of 'observational drawing of resemblances between animal, vegetable and mineral species' (65).
5. Cuvier's *Animal Kingdom: Arranged According to its Organization*.
6. Cf. Bergson, *Matter and Memory*, Chapter 1. A pure perception, as Bergson describes, involves living and perceiving in the present, without any intervention of memory (which, for him, is primarily defined by expectation, interpretation). However, since we do not ever consciously perceive anything without some intervention of memory, however slight, the idea of pure perception is merely theoretical.
7. Perhaps in the manner suggested by Bergson for intelligence to become more akin to instinct.
8. See Paul Klee's *Pedagogical Sketchbook* (16): 'An active line on a walk, moving freely, without goal. A walk for a walk's sake. The mobility agent is a point, shifting its position forward'.
9. In 'Cephalopod chromatophores: Neurobiology and natural history', Messenger (2001) summarizes this difference:

> In all these animals, the term chromatophore refers to a branched cell within which pigment granules can move: the control of such movements is commonly endocrine, although in some groups there is neural control and in others there are both kinds. In cephalopods, however, the chromatophores are organs and they function without any endocrine influence whatsoever.
>
> (Messenger 2001: 476)

10. Cf. the examples I cited in the introduction to this chapter. See also Endler (1981) for a summary of classifications, such as Batesism, Müllerism, crypsis, masquerade, polymorphism and convergence.
11. Hanlon discusses this aspect of his work on his website, Roger Hanlon Visuals (2021).
12. See Flanagan (2015: 311):

> This is not at all to say that verbs provide a didactic model for thinking. And yet their characteristic role in discourse serves as a philosophical heuristic for how things might be understood. Key to this understanding for Deleuze is the sense in which the relationships established by verbs are predicative and not attributive. The difference here is that while attributive relations take place via propositions which only ever express things from the point of view of a subject, the propositions expressed by predicative relations are themselves their own statement on things.

13. See Imperadore and Fiorito (2018) and Hofmann (1907). These articles reflect an 'unpalatable' history of research into the effects of wounding and poisoning of cephalopods, including early records of the manifestation of 'wandering clouds'.
14. Again, as Flanagan (2015) outlines in his discussion of the emergence of 'minor literatures',

> great literature does not so much come about when writers narrate this world (or imagine other worlds) as rather when they give expression to the limits of what can be said of this world. […] Since they come to resemble less and less the very language they draw upon these minor literatures present a challenge to the homogeneity or 'equilibrium' of any one language, and indeed of discourse at all.
>
> (pp. 307–08)

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9

Metamorphosis in Images: Insect Transformation from the End of the Seventeenth to the Beginning of the Nineteenth Century

Janina Wellmann

The English anatomist and discoverer of the circulatory system, William Harvey (1578–1657), was the first person to make a distinction between metamorphosis and epigenesis as two distinct forms of development in Nature. Whereas in epigenesis, the organic forms are created *de novo* successively one after the other, Harvey postulated that they are generated simultaneously during metamorphosis, like a seal impressing its structure on the mouldable material:

> In the generation by metamorphosis forms are created as if by the impression of a seal, or, as if they were adjusted in a mould; intruth the whole material is transformed. But an animal which is created by epigenesis attracts, prepares, elaborates, and makes use of the material, all at the same time; the process of formation and growth are simultaneous.
>
> (Harvey 1965: 335)

Harvey's studies of insect metamorphosis, which were intended to form part of his *Exercitationes de generatione animalium*, were lost during his lifetime (Harvey 1965: 481f.). Whilst his theory of epigenesis was repeatedly discussed, his concept of metamorphosis has so far received little attention (Pagel 1967; Keele 1965; Ruestow 1985: 229–31; Gasking 1967: 16–36; Roger 1963: 112–21). The same applies to the history of insect metamorphosis in the seventeenth and eighteenth centuries or later which remains scarcely studied to this day or restricted largely to individual authors (Ogilvie 2014; Reynolds 2019; Hansen 1907: 173–219; for a short historical comment see Kirby and Spence [1815] 1858: 31–41; an eclectic collection remains with Heselhaus 1953).[1]

In this chapter, I shall look at the development of the concept of insect metamorphosis from the end of the seventeenth to the beginning of the nineteenth century.[2] This time frame has not been chosen at random. On the one hand, it was Harvey's work which was instrumental in introducing the concept of metamorphosis into scientific research. From the end of the seventeenth through the eighteenth century, metamorphosis was regarded as a specific developmental form of the insect group. It was not until the beginning of the nineteenth century that it was recognized as an epigenetic developmental process and part of the newly emerging embryology. On the other hand, microscopy plays a decisive role in the study of metamorphosis during this epoch. The use of the microscope was widespread from the second half of the seventeenth and in the eighteenth century. However, the wealth of different microscopes, individual preparation techniques, methods of observation and, not least of all, highly diverse means of graphic depiction ensured that microscopy remained a heterogeneous research tool until the nineteenth century (Ruestow 1996; Fournier 1996; Wilson 1995). The history of ideas about metamorphosis provides an excellent example for this development.

I shall concentrate here on those researchers who attempted to understand insect metamorphosis with the aid of microanatomy, which merits a special place in the study of the transformation of insects. On the one hand, microscopic anatomy opened up the insect world to scientific research in the seventeenth and eighteenth centuries. By examining the interior of these animals with lenses and microscopes, it was possible to gain totally new insights into their transformation. Whereas insects were considered unworthy of anatomical research at the beginning of the seventeenth century, they became increasingly the focus of interest among physico-theologians who argued that precisely the lowest forms of life were testament to the greatness of God's divine work. On the other hand, microscopic observation raised the question of the role of pictorial representation in a special way. A look at the history of insect research shows that it evolved a rich iconographic tradition from the very outset.[3] Virtually all the major works of natural history published since the seventeenth century have appeared with numerous illustrations.[4] Working with the microscope required new strategies for visualization to an even greater degree. How could the image produced through the lens be transferred to paper? By what means could extremely tiny, complex, dense and malleable structures such as those found in insects be depicted? An even more difficult issue to resolve was how to capture pictorially the transformation of shape which metamorphosis entailed? What exactly changed during observation and how could a picture reflect the entire process of transformation?

In the following, I shall examine the works of three scientists who were active at different phases of the chosen epoch: Jan Swammerdam (1637–80), Pierre Lyonet (1706–89) and Johann Moritz David Herold (1790–1862). One reason for this selection is the fact that the studies by these three were the most elaborate on insect metamorphosis during this period. At the same time, they represent different historical eras: Swammerdam was among the first to deploy the microscope systematically towards the end of the seventeenth century, yet his work was shaped by a mechanistic world view. Lyonet's work, by contrast, is already characterized from the mid eighteenth century by efforts to liberate the living world from the traditional anatomical viewpoint and apprehend its inherent dynamics of development and transformation. Finally, at the beginning of the nineteenth century, Herold was working at a time when biology was becoming emancipated as an independent life science.

Studying their work, I argue that those researchers developed an understanding of metamorphosis through the work with their hand and pencil. I maintain that, up to the beginning of the nineteenth century, the history of insect metamorphosis cannot be written without taking account of the visual representation of metamorphosis. Conceiving metamorphosis meant not only explaining the various stages of transformation but demanded above all the *visualization* of these transformations. I shall show how each of the three authors struggled with the question of how to adequately depict metamorphosis. For them, pictures were an integral element of their work and argumentation. They were tools with which they played and experimented by trying out new techniques of drawing and composing pictures that enabled them to record the changes in an insect's life and thus render them visible.

This does not mean that pictures played the same role for Swammerdam, Lyonet and Herold. On the contrary, all three worked in very different contexts and held quite different views on the extent to which microscopic examination and its depiction were linked with one another. I intend to show, however, that the detailed analysis of how they worked with images and depicted metamorphosis opens up a novel view of the history of insect metamorphosis between 1670 and 1820.

Metamorphosis as a microanatomical drama in the work of Jan Swammerdam

Although predestined by his father to pursue a theological career, Jan Swammerdam turned his attention to science. Throughout his life, however, he remained torn in his scientific work between meticulous, scientific empiricism, on the one hand, and profound piety, on the other hand.[5] This tension was only mitigated by the fact that Swammerdam justified his devotion to insects with his belief that his scientific study of the allegedly lowest forms of animal life brought him closest to God's divine purpose (Swammerdam 1752: 301). In 1669, he published his anatomical studies on the metamorphosis of insects, the *Historia insectorum generalis, ofte*, *Algemeene verhandeling van de bloedeloose dirkens*. In his *Bybel der natuure*, which Hermann Boerhaave published in 1737–38 after a delay of 50 years, he extended his research through the use of the microscope. The subject of both works is the metamorphosis of a long series of insects. Swammerdam compares his studies to the cleaning of a painting:

> Because the true nature of the transformation of these tiny creatures is like a beautiful painting which, having become stained and dirty over time, does not display the true quality of the images it contains but something quite different; and we must [...] consequently restore its original lustre by removing the surface impurities.
>
> (Swammerdam 1752: 2, translation added)

If metamorphosis is thus a painting which needs cleaning in order to perceive it, what role do the 53 elaborate and finely engraved copper plates play which the *Bybel der natuure* contains and which were based on Swammerdam's own drawings?[6] What idea of metamorphosis does Swammerdam conceive in his pictures?

On the action of the anatomist and the nature of transformation

Swammerdam devoted the major part of his pictures to the anatomy of insects, their interior revealed under the lens or with the naked eye, the fine structure of their bodies, their tissues and isolated organs which he displayed both as an illustrator in his drawings and as an anatomist on the dissecting table. But there are also the plates depicting metamorphosis (Figure 9.1A–D). In these plates, Swammerdam shows the 'treatment of the history' of an animal, recounts its 'changes' or its 'slow growth' (Swammerdam 1752, Plate XXXIV, 393; Plate ILIII: 400; Plate XXXVIII: 396; Plate ILVI: 404). Readers are already forewarned in the introduction:

> No one should take exception to the word change or transformation nor let themselves be misled into error. I remind the reader at the very beginning and beseech him to take note that, both here and in the following, I mean by these terms nothing other than a slow and natural growth of the limbs and wish to be understood thus.
>
> (Swammerdam 1752: 2, translation added)[7]

Swammerdam's concept of development evidently corresponds here to the preformationist thinking of his time, whereby all parts of the future organism already

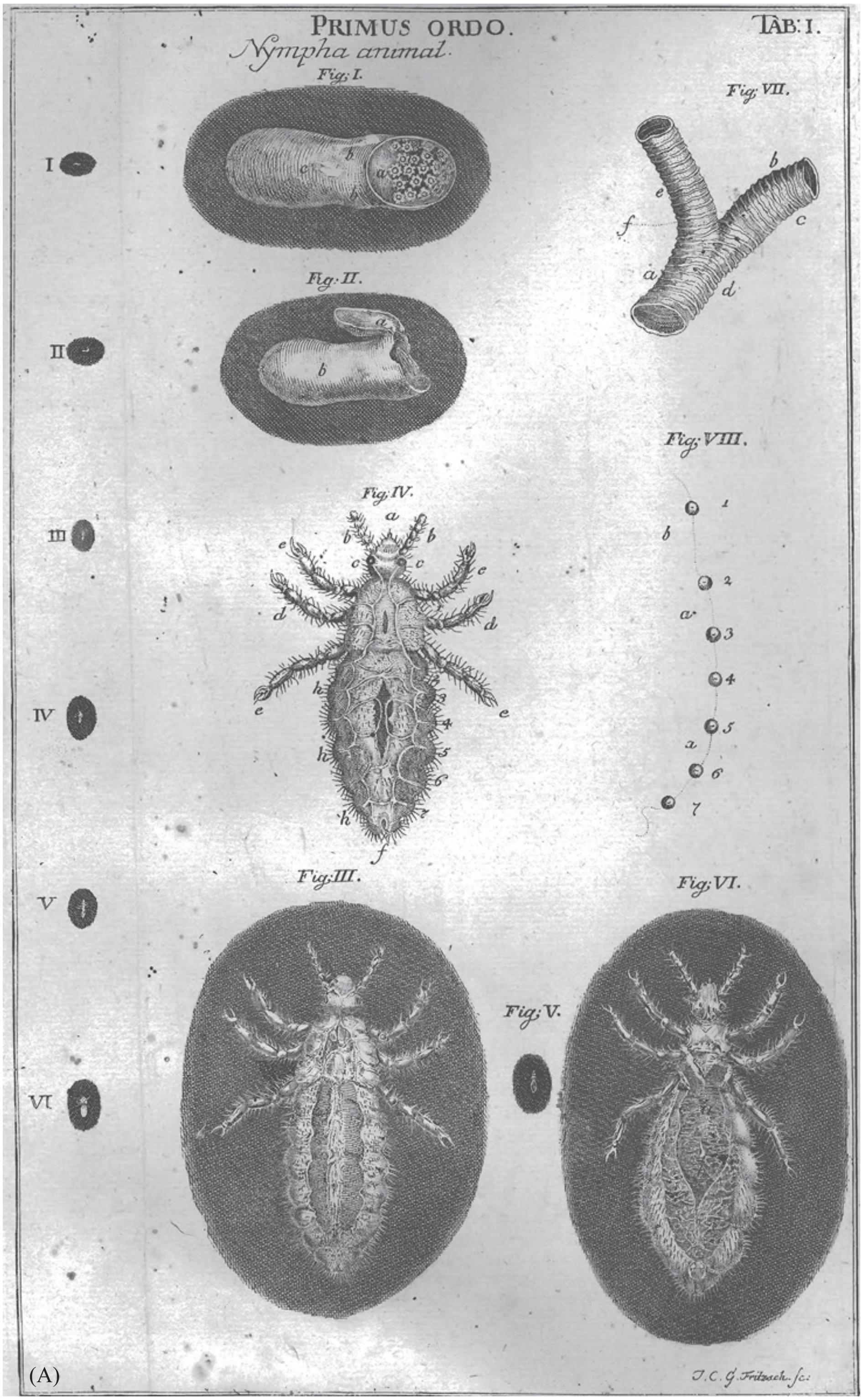


FIGURE 9.1A–D: The four classes of metamorphosis according to Swammerdam (1752: Plates I, XII, XVI and XXXVIII).

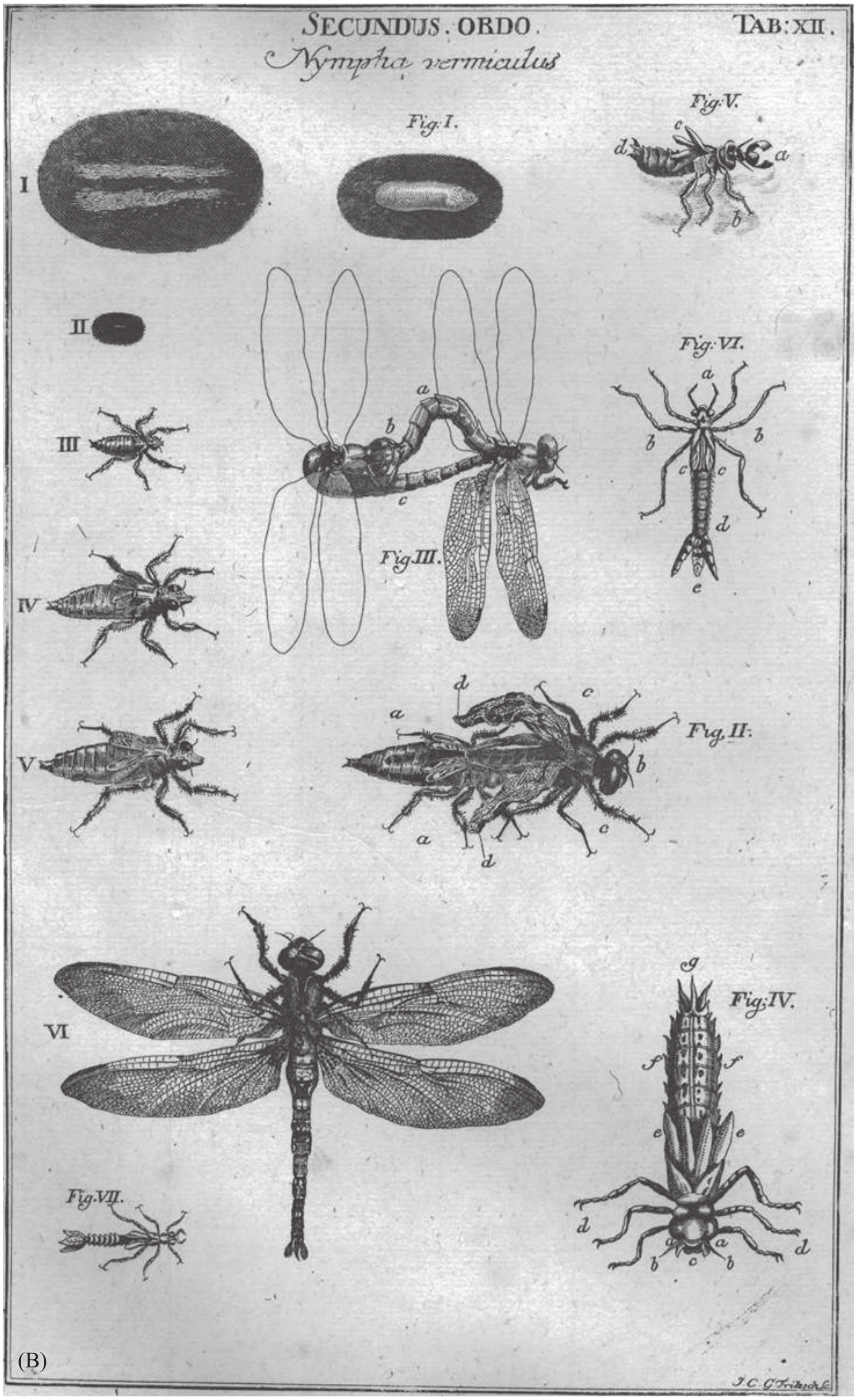


FIGURE 9.1A–D: The four classes of metamorphosis according to Swammerdam (1752: Plates I, XII, XVI and XXXVIII).

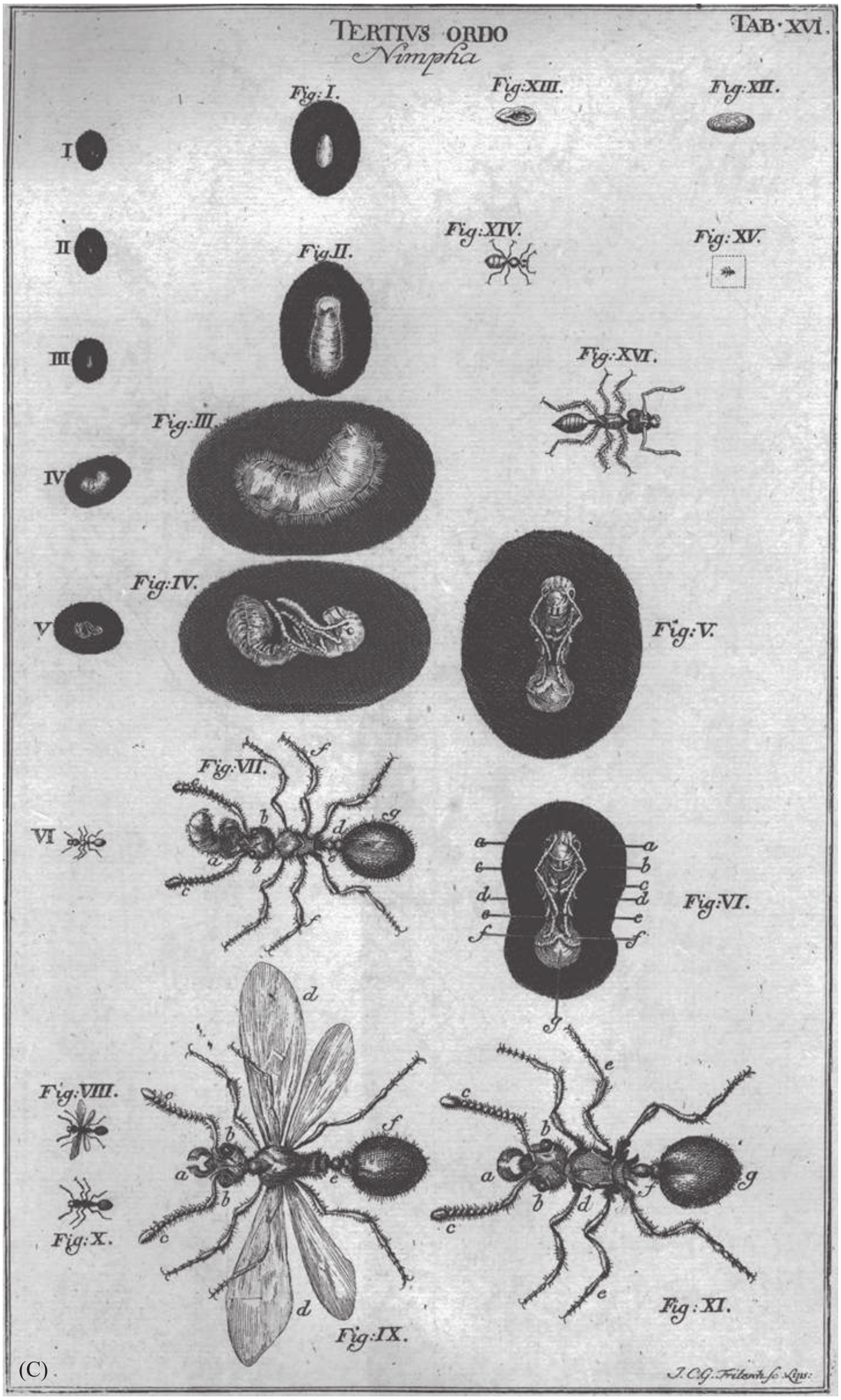


FIGURE 9.1A–D: The four classes of metamorphosis according to swammerdam (1752: plates I, XII, XVI and XXXVIII).

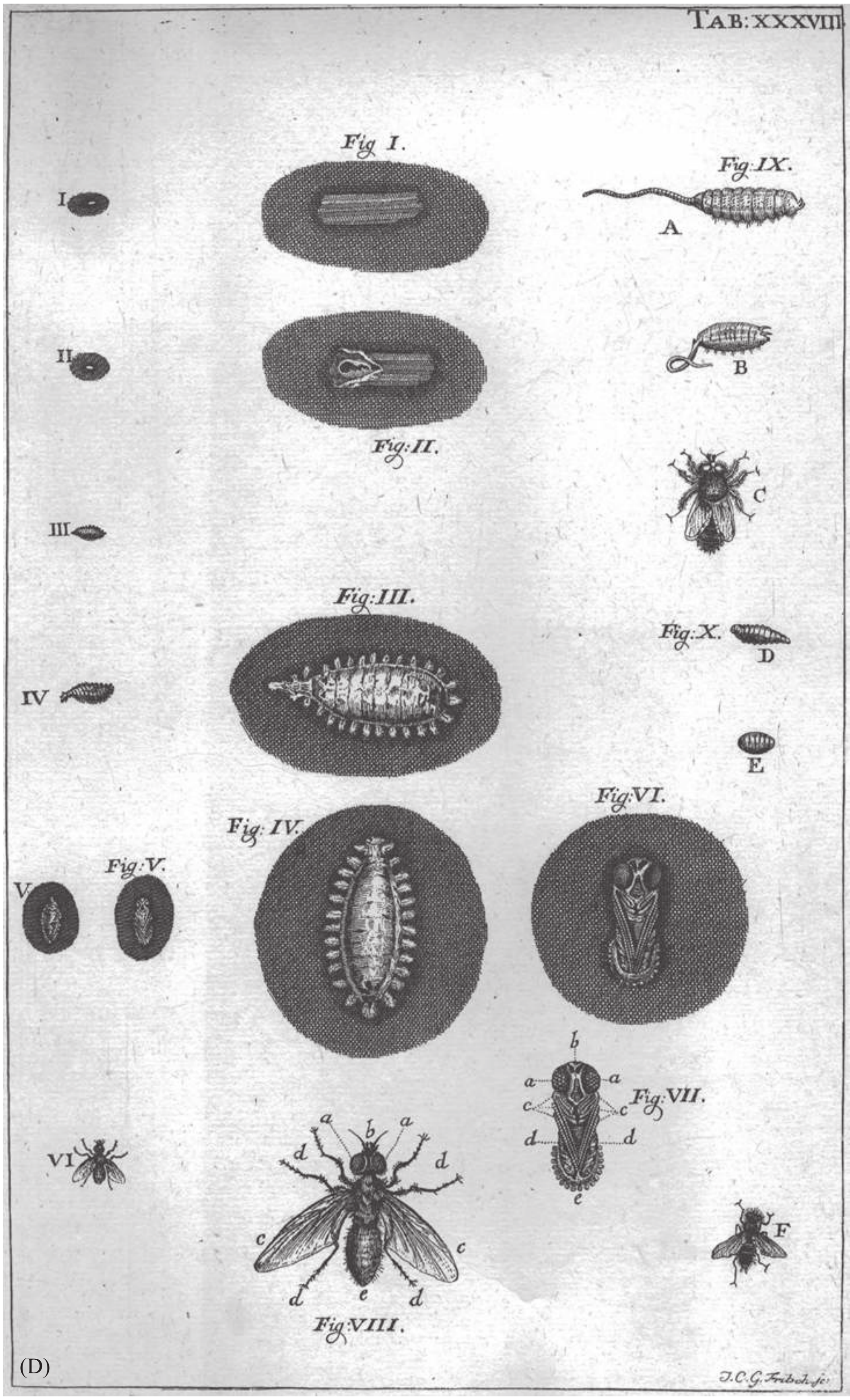


FIGURE 9.1A–D: The four classes of metamorphosis according to Swammerdam (1752: Plates I, XII, XVI and XXXVIII).

exist in miniature in the germ cell and merely become larger and visible in the course of development (Roger 1963; Gasking 1967). The same also applies to metamorphosis. Through his work, Swammerdam wants to show that larva, pupa and imago are *one and the same* animal. What happens during metamorphosis is thus merely a

> sprouting, growing, shooting or expanding of a worm or a caterpillar. […] The worm or the caterpillar do not in fact transform into a pupa but become a pupa due to the growth of their limbs. In the same way, the pupa does not subsequently transform into a winged animal but the very same worm and the very same caterpillar, having taken on the form of a pupa by shedding its skin, becomes a winged animal out of the pupa.
>
> (Swammerdam 1753: 3, translation added)

Swammerdam's research thus has a firm aim from the outset: to make the given visible, reveal the hidden and enlarge the miniature under the microscope. As a result, he faces a special challenge: he must show that caterpillar, larva and imago, which patently differ considerably from one another, are nevertheless similar in each phase of the transformation. The plates on metamorphosis provide a particular body of evidence (Figure 9.1A–D).

In the four plates, Swammerdam classifies the insects according to the completeness of the metamorphosis they are undergoing. The first class covers those insects which are not subject to any further metamorphosis after hatching from eggs, such as lice and fleas. The second group consists of insects whose larvae only differ from the adult imago in that their wings still have to grow or unfurl (e.g. dragonflies). The third class comprises insects which undergo a full metamorphosis, i.e. they first transform into a larva before subsequently entering a pupal stage (like ants) and only then emerge as an adult imago. Swammerdam's fourth and final group, a differentiation from the third, includes animals like beetles, flies and moths which undergo a complete metamorphosis but, unlike the third group, no longer shed their skin (Swammerdam 1752: 17f., 89–93, 115–20, 246–54).[8]

The third class of full metamorphosis includes the butterfly, to which Swammerdam devotes one of the most remarkable plates in the entire book. It not only assembles all the stages of transformation on a single copper plate like those for the individual classes. Plate XXXVII (Figure 9.2) rather stands out because Swammerdam *demonstrates* metamorphosis here in this picture. The picture is the enactment of how he single-handedly transforms the caterpillar into a butterfly, from one developmental stage to the next, under experimental conditions. 'As an encore, I thus want to describe the manner in which a butterfly is embedded in a caterpillar'

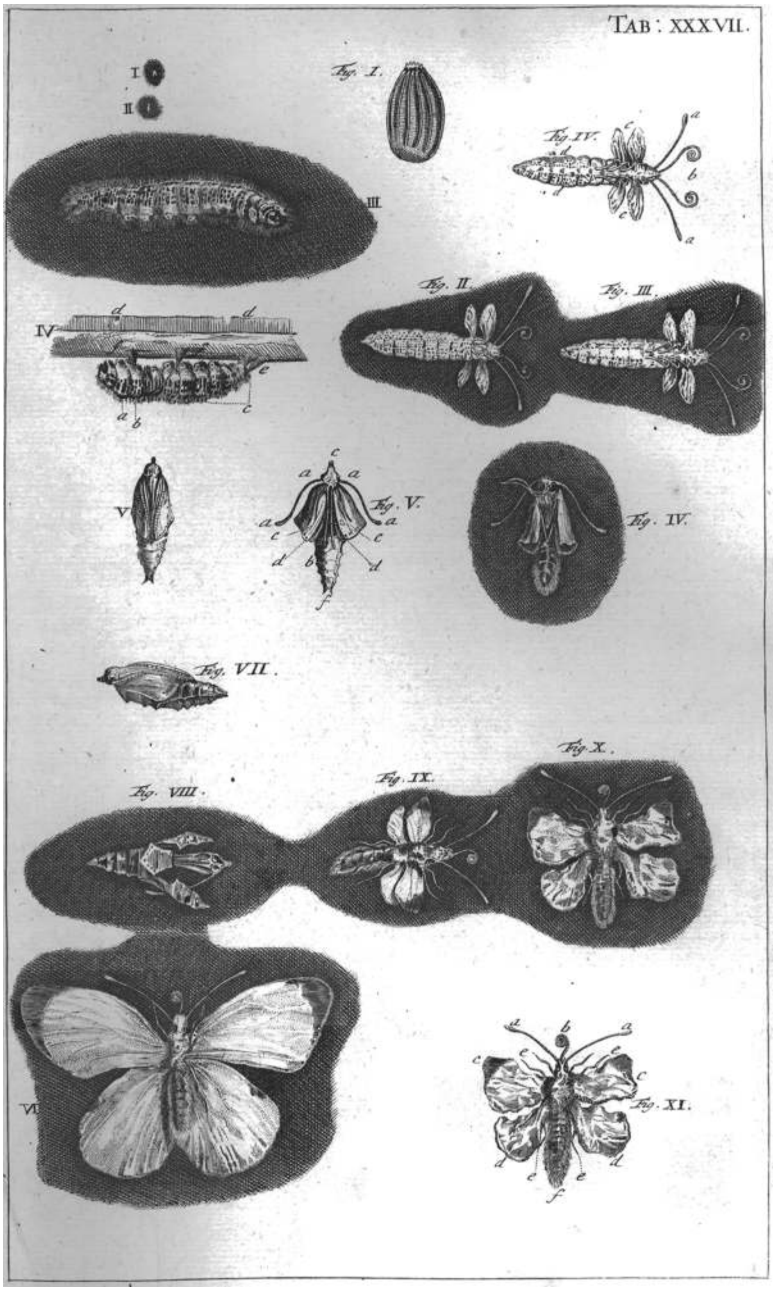


FIGURE 9.2: The metamorphosis of the butterfly in Swammerdam (1752: Plate XXXVII).

(Swammerdam 1752: 241). Put another way: ‘At the same time, I shall show that all the little animals presented on this copper Plate XXXVII are one and the same little animal which is merely hidden in various shapes’ (Swammerdam 1752: 243).

The illustration shows individual figures spread over the copper plate, some of which are depicted as positive and others as negative.[9] The latter stand out particularly against the black background with which the objects contrast. In addition to this optical sub-division of the copper plate, there is a second differentiation through the added letters and numbers: solitary Roman numerals denote the insect ‘in life’, whilst numerals with the adjunct ‘Fig.’ designate the animal in its ‘outline’. As a rule, that is its anatomical duplication, enlarged through the magnifying glass (Swammerdam 1752: 245, 29f.). The vertical arrangement of illustrations I to IV thus shows the various stages of the butterfly from egg to imago in life size: (I) shows the ‘butterfly in the shape of a caterpillar wrapped in its first coat, wherein it is called an egg’, (II) the empty ‘little skin’ after emerging, (III) the caterpillar or ‘the butterfly dressed in the shape of the caterpillar’, (IV) the caterpillar shortly before moulting, (V) the pupa and (VI) finally the completed butterfly (Swammerdam 1752: Plate XXXVII: 395f.). In addition to the vertical arrangement, the plate also has a horizontal sight line. Illustration IV develops from left to right into Figures II to IV (Figure 9.3).

In Figs. II, III and IV (Figure 9.3), Swammerdam shows the ‘butterfly as it is drawn out of the coat of the caterpillar displayed at No. IV’ (Swammerdam 1752: 396). The sequence of figures from left to right thus follows the movement of dissection, the extraction of the butterfly from its shell, the caterpillar. This movement is captured again pictorially in the lower part of the plate, in the sequence of Figs. VIII–X (Figure 9.4).

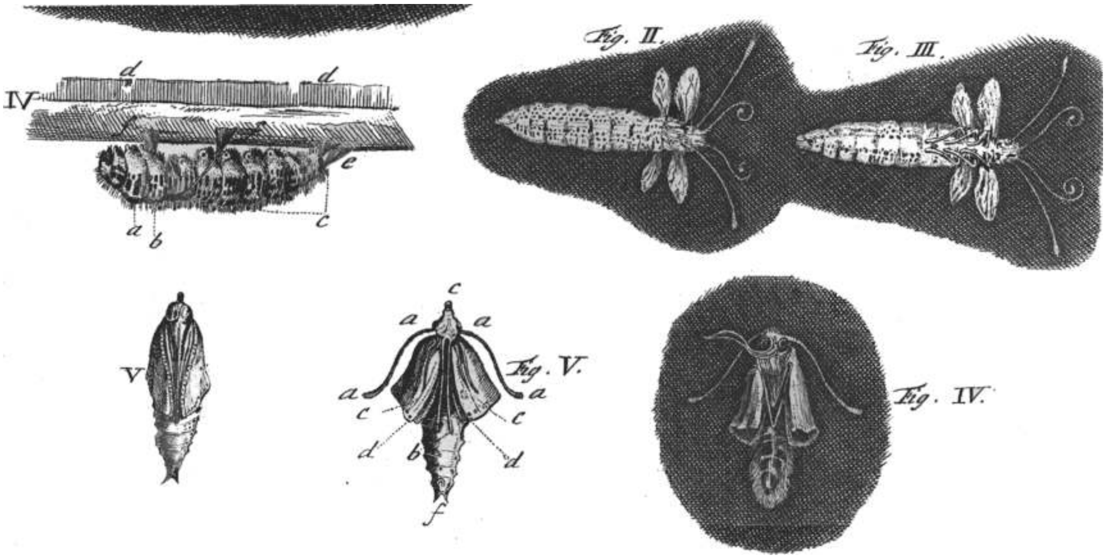


FIGURE 9.3: The sequence of figures II to IV shows how the butterfly can be ‘extracted’ from the caterpillar according to Swammerdam (1752: detail from Plate XXXVII: IV, VI; Figs. II, III, IV and V).

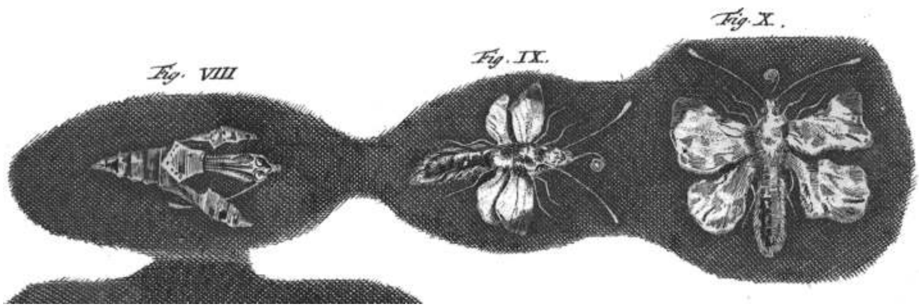


FIGURE 9.4: The emergence of the image from the pupa (Swammerdam 1752: detail from Plate XXXVII: Figs. VIII, IX and X).

This time the sequence of pictures shows the imago emerging from the pupa. The series begins with the empty pupa which the insect has left. This is followed by the freshly emerged animal. Finally, we see the butterfly whose wings are slowly unfolding.

The picture composition suggests that the two processes represented are a qualitatively comparable procedure: the sequence of three figures each is arranged in parallel, develops from left to right and the presentation on a black background (with the exception of No. IV, which nevertheless largely corresponds to No. 3 above it) optically reinforces the linear chain of the images. In fact, the natural process of emergence at the end of the butterfly's metamorphosis is represented in the second case whilst the artificial 'extraction' of the butterfly from the caterpillar by the anatomist is in the first case. That this is by no means a comparably natural act is clear from a more precise description of Swammerdam's procedure which has made this 'extraction' possible:

> In order now to prove irrefutably that the butterfly is present within the skin of the caterpillar, one may now use the following technique. One takes an adult caterpillar, ties it to a fine thread and immerses it several times in boiling hot water, but withdrawing it rapidly each time. The caterpillar's outer skin will then peel off from the inner which surrounds the butterfly.
>
> (Swammerdam 1752: 242, translation added)

Swammerdam was indeed one of the most skilful microanatomists of his time (Ruestow 1996; Bodenheimer 1928: 342–65). Hermann Boerhaave portrays Swammerdam's tools in his introduction to the *Bibel der Natur*. He describes his examination table with its 'brass arms', 'which could be turned, raised and lowered as one wished', his 'incredibly fine and sharp scissors', 'knives, lancets and stillettoes, which were so small that he had to sharpen them under a magnifying glass', as well as the ‘little tubes’ as fine as hairs with which Swammerdam injected ‘dyed liquids’ and ‘inflated’ the insect body (Swammerdam 1752: X, XI, also 9, 17).[10] Swammerdam preserved the insects prepared in this way, ‘frozen’ so to speak in each stage of its development and built up an immense collection:

> I also possess some worms and caterpillars, different gold pupae and some worms which are half caterpillars and half gold pupae. I can thus also demonstrate after life how the butterflies lie in miniature in their last skin […], with all their colours […]. Furthermore, [I] keep the antennae, intestines, stomachs and mouthparts of the butterflies.
>
> (Swammerdam 1752: 220, translation added)

Boerhaave reports how Swammerdam staged the metamorphosis of the insects as a drama with the aid of this collection:

> With such skill, intelligence and tools […], he finally brought things so far that, as often as he wished, he could visually demonstrate the nature of the enshrouding and development of the transforming bodies of the little creatures. He could at will transform the caterpillar into a pupa, accelerate, stop, interrupt and steer its moulting. What he saw, he claimed and what he claimed he manifestly proved.
>
> (Swammerdam 1752: X, translation added)

Metamorphosis is here the result of anatomical dissection and preparation.[11] Anatomy not only allowed the examination to be separated from the natural development process. On the contrary, it created a completely new observer situation that could be updated, repeated and reversed at any time. The researcher rather than the insect becomes the actor and Swammerdam announces: ‘Yes I can, if I wish, transform a caterpillar into a gold pupa’ (Swammerdam 1752: 9, also 17). Plate XXXVIII (Fig. 9.2) shows this kind of transformation: it equates the anatomical act of dissection with the natural act of metamorphosis. Here the anatomist becomes the imitator of Nature who can himself produce metamorphosis via anatomy and thus prove the continuity between the various stages. Swammerdam achieves this impression on the plate by linking the horizontal and vertical sightlines with one another. From top to bottom, the picture sequence I–VI reveals the development from egg to adult butterfly. The respective connection of these stages then results from looking right, to the anatomical ‘outline’. The viewer reads in a zigzag pattern, as it were: he links the natural order of the individual insect stages with one another via the anatomical dissection. Correspondingly, anatomy appears as the natural explanation for metamorphosis in the illustrations. However, the picture which Swammerdam draws here of metamorphosis is the picture of a non-transformation. It presupposes that in each individual stage 'the shape of the future animal and its limbs can be perceived', i.e. that the individual organs and structures are always recognizably similar (Swammerdam 1752: 4). Swammerdam's depiction is based on the similarity, the comparability of what has been observed, in order to optically equate the violently extracted and naturally emerged body. But a transformation whereby completely new structures are created, new forms evolve or existing ones are replaced, also requires other representational techniques to elaborate the continuity of the body beyond mere similarities. In other words: that 'very beautiful painting' with which Swammerdam earlier compared metamorphosis not only had to be cleaned. Ways and means to paint it had to be found first.

The perfect picture. Pierre Lyonet's anatomy of the caterpillar

The *Traité anatomique de la chenille qui ronge le bois de saule* from 1762 is one of the most significant works on insect microanatomy in the eighteenth century. Here too, pictures are of central importance.[12] Pierre Lyonet was predestined for such a work since he had trained not only as a draughtsman but also as a copper plate engraver. He was first a pupil of the portrait painter Carel de Moor. Through his acquaintance with the painter Hendrick van Limborch, Lyonet became a member of the guild Confrérie Pictura of The Hague in 1733. There he also learned drawing from a model and cast under Jan van Gool. His first encounter with engraving was in the 1740s. Trembley reports in his *Mémoires* that Lyonet began copper plate engraving after just one visit to Jan Wandelaar (1690–1759), who created the famous engravings for Albinus' anatomy (Trembley 1744: VIII).[13]

Before Lyonet became famous with his own *Traité*, he had already made a name for himself as an artist. In 1742, he published the French translation of Friedrich Christian Lesser's *Insecto-Theologia*, which had appeared in German without illustrations in 1738. He not only published the work with his own additions but made drawings which he had engraved in copper by Jakob van der Schley. The first work with Lyonet's own engravings was Abraham Trembley's *Mémoires pour servir à l'histoire d'un genre de polypes d'eau douce,* which appeared in Leiden in 1744. He produced all the drawings for the plates, however, only engraved the last eight plates himself. Lyonet also made three engravings for Johann Nathanael Lieberkühn's *Dissertatio anatomico-physiologica* (1745).[14] He planned a detailed anatomical study of the willow caterpillar, for which he abandoned a natural history of the insects of The Hague he had already started, because he considered this topic 'sufficiently difficult to leave the field free for me' (Lyonet 1762: IV). Lyonet began his dissections in 1745. Initially, he only made drawings of them. It was not until 1757, after a hiatus of six years during which he served the Dutch government as a decipherer of diplomatic correspondence, that he resumed the work and needed two years to complete the copper plates (Seters 1962: 67–71).[15]

Metamorphosis as inner transformation

The treatise on the anatomy of the caterpillar was only the first and 'least' of a total of three planned tracts: a second and third on the anatomy of the pupa and the butterfly were supposed to follow (De Haan and Lyonet 1832: I). Lyonet's work remained unfinished and some of his preliminary works were only published posthumously in 1832. The crucial point is that his project was not aimed at an anatomical description of the caterpillar solely for the sake of its anatomy but rather at 'following the successive interior changes which the pepper-and-salt moth undergoes whilst preparing to become a chrysalis and during its pupal state to transform into that of the winged insect' (De Haan and Lyonet 1832: I). Lyonet is already departing here from the preformationist theory without yet adopting a clear alternative position. Instead he seeks a solution through the pictures.

Although Lyonet was unable to complete the project, he had taken his studies so far that he had recognized metamorphosis as a process of dramatic transformations inside the caterpillar: a series of 'admirable and almost universal changes which the entire interior organisation of the caterpillar undergoes in order to become a butterfly' (De Haan and Lyonet 1832: 544). Lyonet's approach is to break down the transformation as such into a series of distinguishable subprocesses. He differentiates between six central transformations in total. The most conspicuous is first 'the complete transformation of the caterpillar's exterior form' (De Haan and Lyonet 1832: 544). Second, he observed 'the dissolution of more than four thousand muscles which dissolve within a few days during the metamorphosis' (De Haan and Lyonet 1832: 544f.) Then comes third 'the dissolution of two external sheaths' of the bronchia (De Haan and Lyonet 1832: 545). Fourth, Lyonet mentions the changes to the nervous system, where most of the nerves disappear as they lose their function and the remaining nerves receive new tasks (De Haan and Lyonet 1832: 545). The fifth change concerns 'the production through intussusception of an innumerable quantity of channelled scales with three edges' (De Haan and Lyonet 1832: 546). The sixth change is also the most remarkable: 'the production of close to twenty-one thousand telescopes' which form the butterfly's compound eye and take the place of the caterpillar's twelve eyes which were constructed in a completely different manner (De Haan and Lyonet 1832: 546).

For Lyonet, pictures are the pivotal element for understanding metamorphosis. He stresses that there is so far no work 'whose illustrations, which do not make up the least essential part, are suited to satisfy the eyes that are so little illuminated about these kinds of objects' (De Haan and Lyonet 1832: I). Although unable to finish his illustrations on metamorphosis, Lyonet developed a pictorial language in his *Traité anatomique* which fulfils all the requirements to represent metamorphosis in a novel manner. The precision of representation which Lyonet strove for in his treatise pursued not only the ideal of a mathematical exactness (Stafford 1996: 254) but also the approach that the changes during metamorphosis could only be followed if one succeeded in representing the internal structures of the caterpillar as a fabric of miniature, connected and coordinated units. Only when this interior topography is precisely recorded will it be possible also to comprehend the many small changes that lead to structures changing their position, breaking loose from old connections and entering into new ones as a complete internal transformation. In order to achieve this precision, Lyonet utilizes a series of new picture techniques.

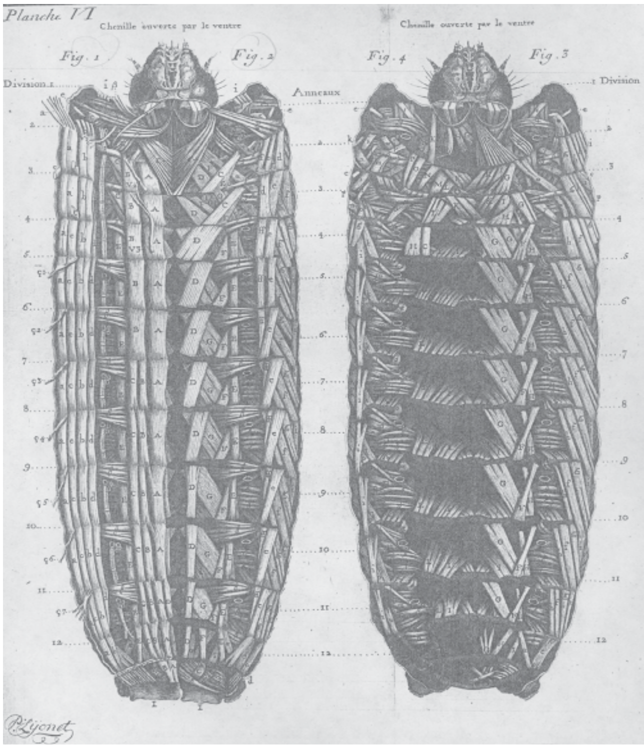
On the location of seeing: The *lignes idéales*

Lyonet strove for the perfect picture – the picture in which everything was visible, which recorded every vessel, every trachea and every individual muscle inside the caterpillar. The picture shown by previous research, including that by Swammerdam, Réaumur, Malpighi and de Geer, was merely 'extremely simple figures and largely formless' (Lyonet 1762: XXI) and nothing more than 'the work of daubers' (Letter to Réaumur, quoted in Hublard 1910: 65). Lyonet demanded more of himself: 'I have taken exactness to such a point […] I do not believe I could have taken it any further than I have done' (Lyonet 1762: VII). He himself calculated what that meant: 228 muscles of the head, 1647 of the body, 2186 of the intestinal tract, a total of 4061, minus those counted twice, making 4041 muscles alone for which he was supposed to find space in his pictures – not to mention all the other structures inside the caterpillar (Lyonet 1762: 584).

This interior complexity posed a representational problem for Lyonet. Naming all the individual structures was out of the question: 'that would have been crazy. Ten thousand names would not have sufficed. It would have required a dictionary to find them' (Lyonet 1762: VII). Apart from some important, recurring structures which receive a name, the others are therefore identified with 'letters, marks or numbers' (Lyonet 1762: VIII). But the letters and numbers do not guarantee a clear location and allocation to the respective structures depicted. A vestige of imprecision remains in the reciprocal reference between picture and letter – a practice adopted in the early days of anatomy. Lyonet solves this problem: he invents a genuinely graphic element, the *lignes idéales*. These lines form a kind of topographic mesh which Lyonet places over the illustrations. They function like those numbers, letters or other marks. But rather than being beside the picture, they are an intrinsic part of it: they designate the place where the eye must search within the picture. Unlike linguistic terms, the *lignes idéales* are not completely arbitrary. On the one hand, they are notional, imagined lines; on the other hand, Nature itself – for example, in the segments of the insect's body – has suggested them: 'It appears as if Nature itself had taken care to provide them and secure them in all types of caterpillar with markings which are usually very easy to recognise' (Lyonet 1762: 21).

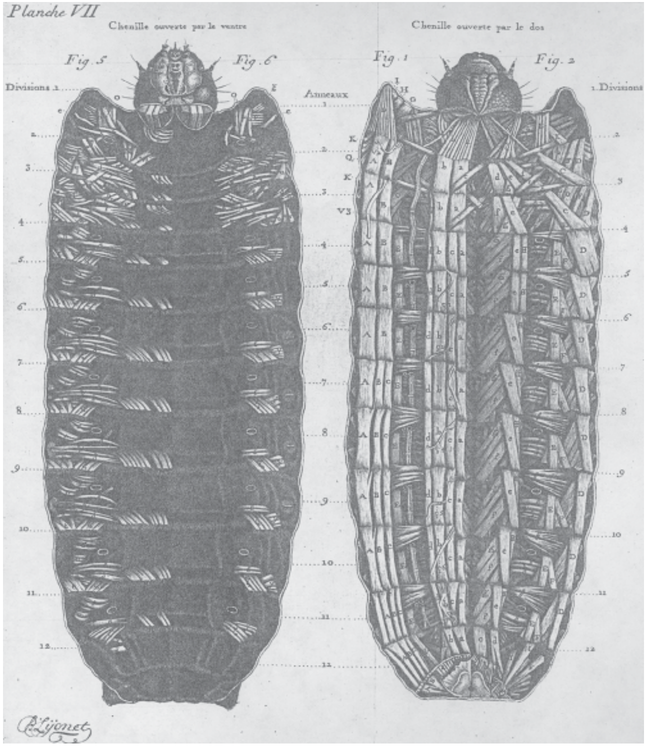
The *lignes idéales* thus form a mesh of vertical and horizontal lines which are partly selected at random and partly follow the natural segmentation or vessels of the insect's body (Figure 9.5A–C). In this way, eight lines form a grid of 104 fields altogether, in which each structure within the caterpillar can be precisely pinpointed:

> The eight longitudinal lines […] together with the twelve transversal lines, which I have called divisions, split the caterpillar, including the head, into 104 parts and provide, thus planned, a comfortable means to designate the places about which one wishes to speak and to locate them without the aid of any letter.
>
> (Lyonet 1762: Chapters 2 and 25, translation added)

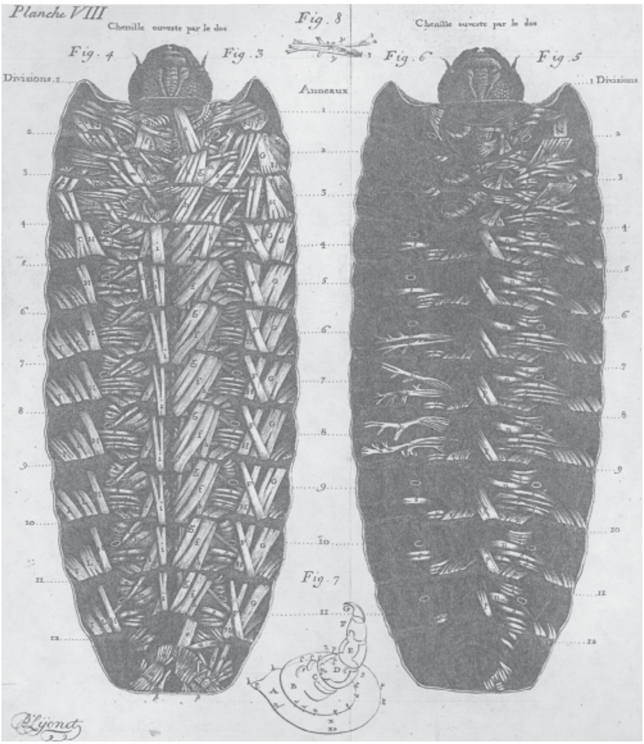


(A)

FIGURE 9.5A–C: The anatomy of the muscles of the caterpillar of the pepper-and-salt moth (Lyonet 1762: Plates VI, VII and VIII).



(B)



(C)

FIGURE 9.5A–C: The anatomy of the muscles of the caterpillar of the pepper-and-salt moth (Lyonet 1762: Plates VI, VII and VIII).

The individual structures are quasi duplicated by the grid of the ideal lines – they are represented both as tissue and in the coordinate system of the lines. What is depicted and its description are overlaid, as it were, and pictorially merged. That has a central consequence for Lyonet's further course of action: the *lignes idéales* are a key means of dissolving the body into layers. Each structure is present in the picture even when it is absent; it has its place beyond its current representation. Another graphic procedure which serves this purpose is to depict each of the caterpillar's various tissues using a different engraving technique. Lyonet thus represents the caterpillar's fat with dots known as stippling, the muscles with linear hatching and the bronchia with transverse arches (Lyonet 1762: X).

The muscles provide an example of the specific effect this has on the pictures (Figure 9.5A–C). Due to their uniform linear hatching, Plates VI, VII and VIII are highlighted 'at a glance' as a coherent unit and delineated from the other plates (Lyonet 1762: VIII).

The sequence of Plates VI–VIII is devoted to the caterpillar's muscles. Each plate shows two caterpillar bodies. A total of six, equal in size and with the same tissue hatching, are placed side by side against a white background. On closer examination, it becomes apparent that although they are iconographically very similar, the internal structure of the caterpillar bodies varies. Only the muscles are depicted with linear hatching; all other organ structures are blanked out. However, this act of reduction only creates the prerequisite for the new complexity which Lyonet strove to achieve in the plates. Above the six caterpillar bodies, a line of text explains 'caterpillar opened from the stomach side' or 'caterpillar opened from the back side'. Thus the first three figures (cf. both figures on Plate VI and the left figure on Plate VII) show the opened caterpillar from the stomach side, the following three figures (cf. the right figure on Plate VII and both on Plate VIII) give a back view. In addition to the change from front to back view, another peculiar differentiation between these views becomes apparent: each individual depiction of the opened caterpillar is divided once again down its longitudinal axis into two parts, which Lyonet calls 'figures'. The front and back views are thus each subdivided into six figures. Instead of six caterpillar bodies, the observer is presented with twelve half-figures, or more precisely two times six. What initially seems like an interior view of six opened caterpillars is actually a composite: what one sees on the plate is not *one* prepared caterpillar body but two, which are merged into a single body along the *ligne supérieure*. What appears pictorially as a single entity is de facto a dissection sequence: one half of the caterpillar shows the muscles at a moment of anatomical dissection, the second shows the subsequent step of the dissection which now reveals the layer of muscle which was still hidden by the first. Lyonet writes the following:

> The muscles which appear fully uncovered in one figure have been removed in the following figure in order to show the muscles they covered. As a result, one sees new letters designating the new muscles each time in the first to the sixth figure: and if one sees the same letter on the same ring in two figures, then that is the certain marking of the same muscle which has not yet been removed.
>
> (Lyonet 1762: 'Explication des Figures', Plates VI, VII and VIII: 39, also 114, translation added)

The pictures are a kind of in-depth preserved specimen and pursue the exposure of ever newer structures as they penetrate deeper into the body. But even more they are a pictorial record of the dissection process. They permit a dynamic view of the specimen. As the gaze wanders to and fro between the halves, it establishes relations between the muscles and permits it to follow how the topography changes during the dissection. The once anatomically rigid body is here taken further into a structure of potential options. The view into the depth of the caterpillar thus at the same time opens up the pictorial space for the temporal development of structures during metamorphosis.[16]

Lyonet is convinced by the layout of his pictures: 'solely with the aid of such figures, incidentally, can one produce an accurate idea of the things' (Lyonet 1762: XXI). At the same time, he is aware of the disturbing nature of his pictures. He knows they 'do not resemble at all' the pictures of traditional anatomy (Lyonet 1762: XXI).[17] Indeed, Lyonet brought anatomy into a new pictorial form: first, he created a form where the animal was dissected but did not fall to pieces. In Lyonet's work, the viewed object does not dissolve under the anatomist's knife, so to speak, and disintegrate into the individual parts of a unit which is no longer coherent. On the contrary, the integrity of the caterpillar remains preserved. Regardless of the ever deeper penetration of the insect's muscle and tissue layers, the body continues to exist as a whole. Although dead and dismembered, the picture shows the caterpillar's intact form. Second, this new form brought the anatomist's procedure into the picture itself: the picture both conceals and exposes the anatomical act at the same time. The individual steps of the dissection become visible across the three plates, whilst the viewer's gaze repeatedly reassembles the various levels and thus remains directed at the animal's overall unity.

By merging the figures into an apparently single insect body (instead of representing them as two separate halves), Lyonet blends anatomical analysis and intactness together. In contrast to Swammerdam, Lyonet's plates represent the attempt to capture the dynamics of a process in pictures. The sequence of pictures, the graphic dissolution of the body into layers through the *lignes idéales*, the isolation of a single structure using the hatching technique: all these are pictorial instruments which provided the basis for representing metamorphosis. Whereas Swammerdam still wanted to 'clean' the finished painting of metamorphosis which was 'sullied' by false ideas about an actual transformation, Lyonet tried to understand this transformation. The 'drawing pencil' was supposed to lay the foundations for being able to draw the 'admirable changes' by 'sketching with a steady hand the details of an insect's interior parts before and after its transformation, following it from one form to the next in its passage' (Lyonet 1762: XVII). Lyonet's approach was initially not adopted by others. It was not until 50 years later that a German natural scientist began a study which resembled Lyonet's intentions in many respects.

From picture to picture series: Johann Moritz David Herold's Developmental History of Butterflies

Johann Moritz David Herold's *Entwickelungsgeschichte der Schmetterlinge* (*Developmental History of Butterflies*) appeared in 1815. Despite the emergence of biology as an independent science of living things and the establishment of the epigenetic concept of development, knowledge about the processes inside insects during metamorphosis was still very scant. Herold felt that what Swammerdam and Lyonet had furnished was 'really just a fraction' since they had 'noted almost nothing at all about the changes which occur within the organisation during the transformation of caterpillars into pupae and these into butterflies' (Herold 1815: IIIf.).

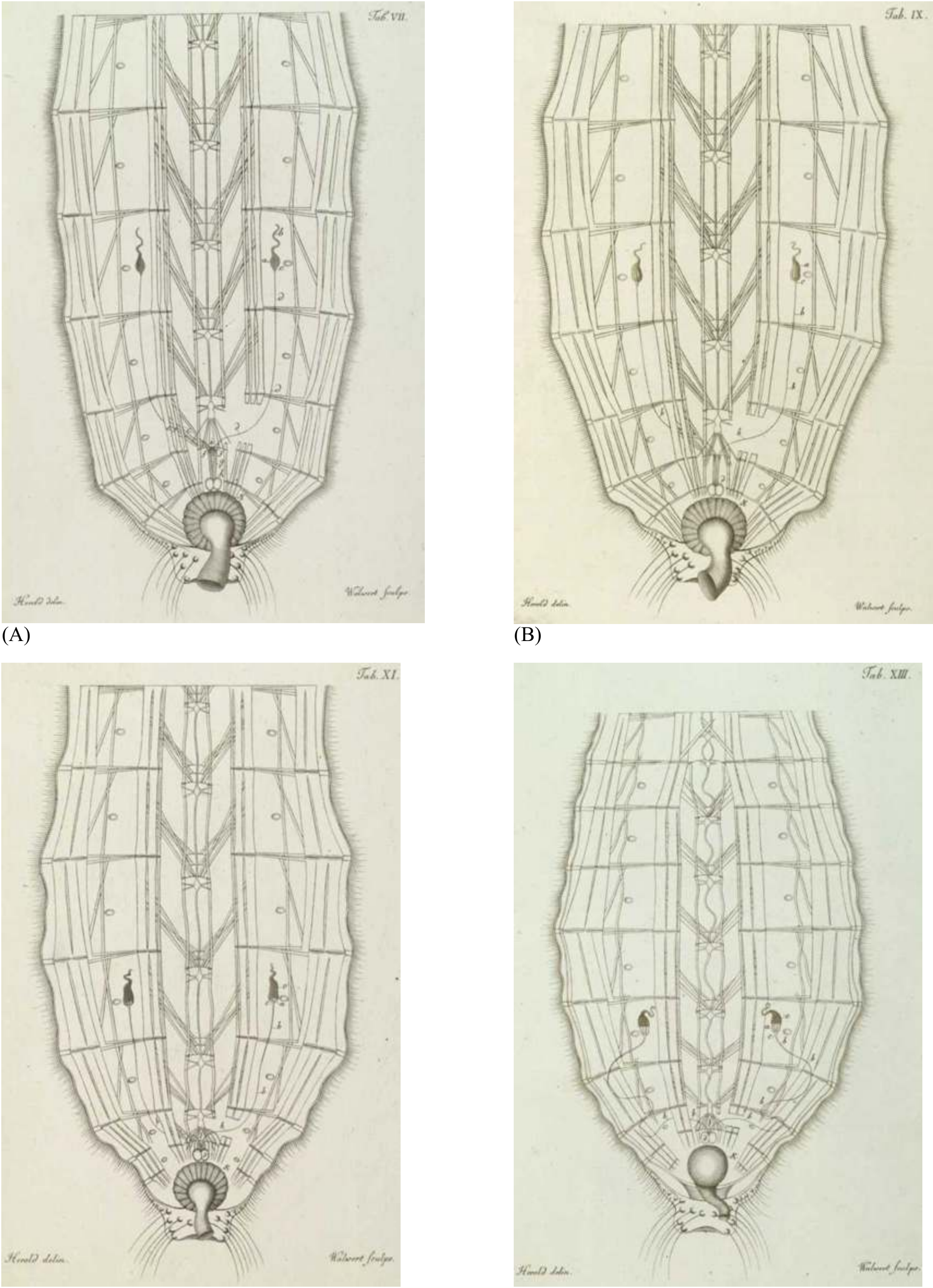
Johann Moritz David Herold is a largely unknown figure in the history of science. His brother-in-law, Ernst August Daniel Bartels, professor for anatomy and obstetrics in Helmstedt, had a substantial influence on Herold's career. After starting medical studies at the University of Jena in 1806, Herold switched the following year to Helmstedt where his brother-in-law taught him. In 1809, he was appointed prosector working for the anatomist Johann Friedrich Meckel the Younger (1781–1833) at the University of Halle. In 1811, Herold moved to Marburg where he continued his scientific career until his death. In recognition of his work on the developmental history of butterflies, Marburg University made him an associate professor of medicine in 1816. Herold became a full professor of medicine in 1822, then finally professor for natural history and director of Marburg's zoological institute in 1824. Instructed by Meckel in the dissection of lower animals, insects remained Herold's real passion right up to his death. After completing work on the developmental history of butterflies, he planned a developmental history of invertebrates. With the first part of *Studies on the History of the Formation of Invertebrate Animals in the Egg* (1824) devoted to spiders, Herold provided the first work on the embryology of spiders. A sequel to this work appeared posthumously as part of Herold's literary estate, published by Arnold Gerstenacker in three parts in 1835, 1838 and 1876 under the title *Studies on the History of the Formation of Invertebrate Animals in the Egg. On the Generation of Insects in the Egg.* Although Herold made a major contribution to the embryology of lower animals with these works, their significance for the history of science has not been properly recognized to this day.[18]

However, the *Developmental History of Butterflies* from 1815 can be regarded as Herold's main work, in which he adopted completely new methods of studying his objects. The caterpillar of the large cabbage white butterfly (*Papilio brassica L.*) was the focus of his attention. He restricted himself to studying the caterpillar, disregarding the embryonal stage due to the small size of the eggs and the associated difficulty of observing them. In 1811, he had made the discovery that within the caterpillar it was already possible to distinguish the gender-specific predisposition for the future reproductive organs (Herold 1815: V). Based on this discovery, Herold formulated a new concept for the transformation of insects: he represented the caterpillar's metamorphosis by concentrating on the genesis of a single structure, namely the reproductive organs. To this end, Herold used a new pictorial representation of metamorphosis: the picture series.

The picture series

Developmental History of Butterflies contains a total of 33 coloured copper plates. The pictures were drawn by Herold himself and engraved by Jakob Samuel Walwert (1750–1815), a draughtsman, copper plate engraver and miniature painter from Nuremberg (Schwemmer 1974: 53).

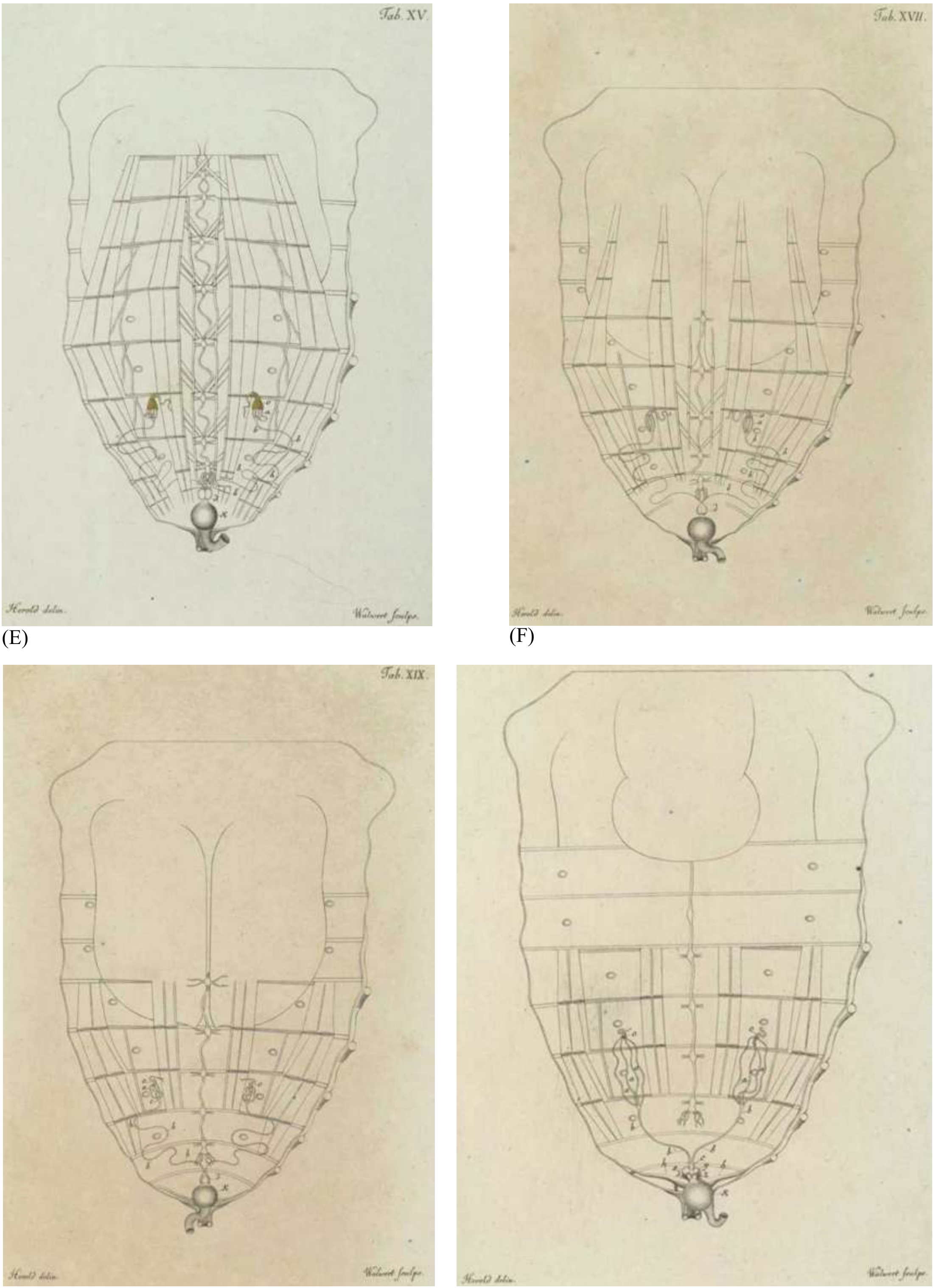
Lyonet's work was dominated by the ideal of the wealth of detail in the picture which reproduced the complexity of the insect's interior in a dense drawing. Herold chose the exact opposite procedure: he emptied the individual picture but instead multiplied the number of pictures. Thirteen plates show the transformation of the male reproductive organs and fifteen the female (Figure 9.6A–O). In the book, plates of the male and female reproductive organs are bound alternately one after the other. This juxtaposition made it possible to reveal the differences in the male and female development which Herold was the first to recognize and which he considered his key discovery. But the pictorial arrangement of the plates permitted another quite different order, namely to track the caterpillar's 'type of development' (Herold 1815: 12). In order to follow the emergence of the female reproductive organs, the viewer should stick to the sequence of the plates 'Tab. XXI, Tab. XXIII, Tab. XXV, Tab. XXVII, Tab. XXIX, Tab. XXX' (Herold 1815: 12). So instead of looking at the plates alternately, the viewer should only observe the plates of the male or the female caterpillar respectively.



(A) (B)

(C) (D)

FIGURE 9.6A–O: Herold depicts the development of the male reproductive organs of the caterpillar of the large cabbage white butterfly (Herold 1815: selection from Plates VI–XXXII).



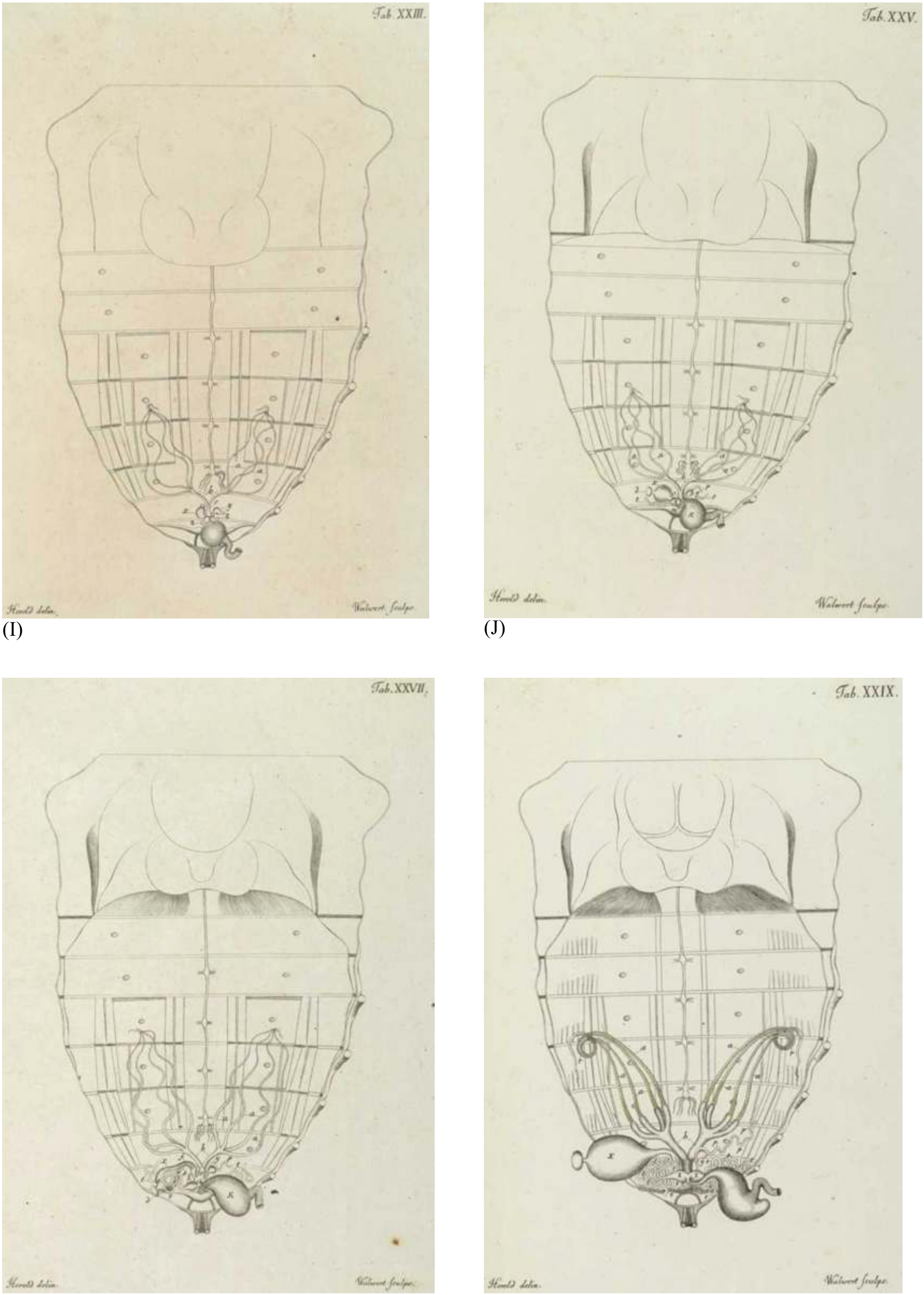
(E)

(F)

(G)

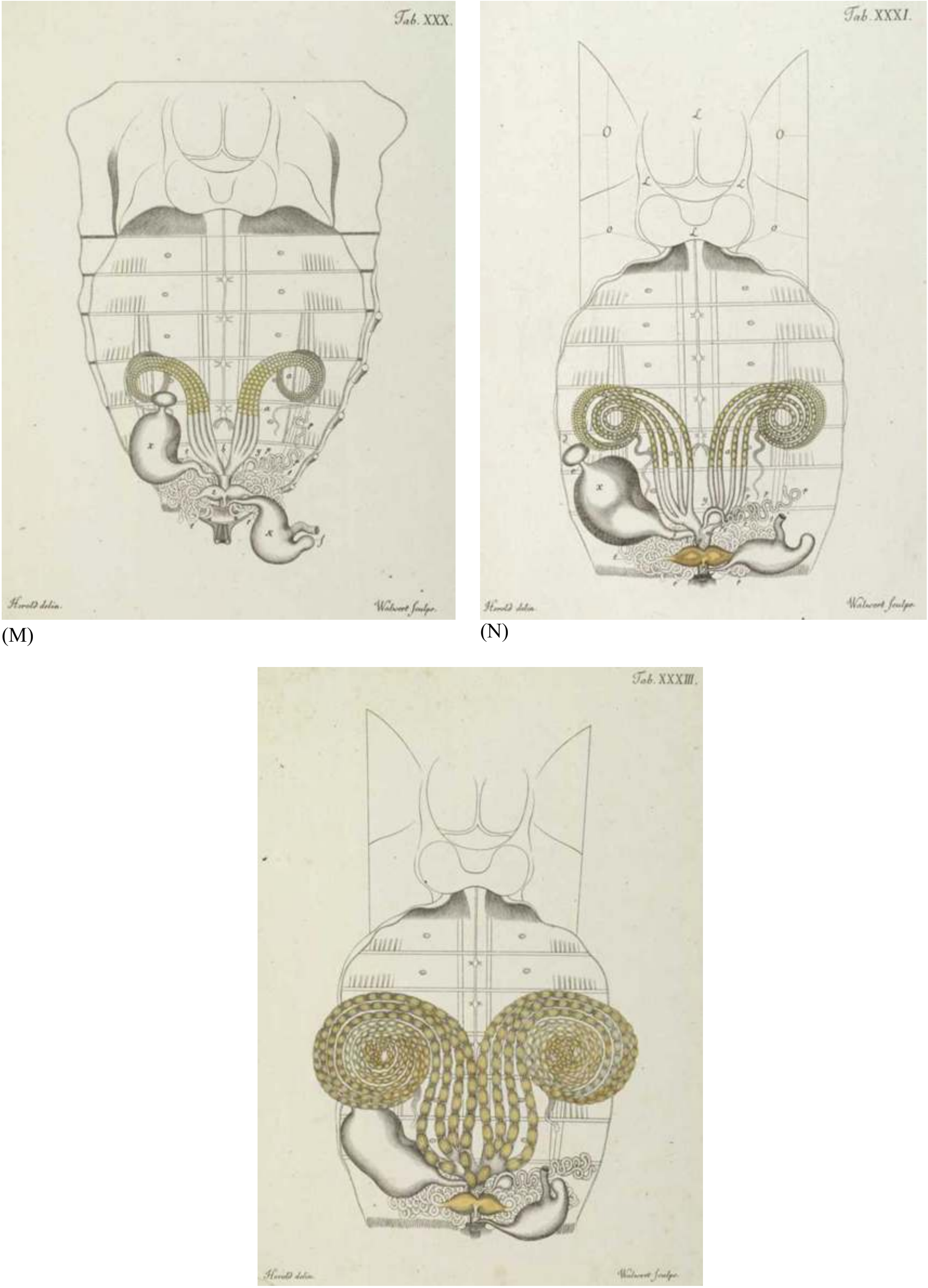
(H)

FIGURE 9.6A–O: Herold depicts the development of the male reproductive organs of the caterpillar of the large cabbage white butterfly (Herold 1815: selection from Plates VI–XXXII).



(I) (J) (K) (L)

FIGURE 9.6A–O: Herold depicts the development of the male reproductive organs of the caterpillar of the large cabbage white butterfly (Herold 1815: selection from Plates VI–XXXII).



(M)

(N)

(O)

FIGURE 9.6A–O: Herold depicts the development of the male reproductive organs of the caterpillar of the large cabbage white butterfly (Herold 1815: selection from Plates VI–XXXII).

The design of the plates makes this visual elaboration of the transformation possible: the selection and the concentration of the pictorial elements are their outstanding characteristic. First, the use of colour (which we also encounter again in Baer's *Developmental History* of 1828) guarantees maximum attention. The caterpillar's male reproductive organs are highlighted in red, the female reproductive organs in yellow: more precisely, the change in their appearance and their migration within the caterpillar's body during metamorphosis. In addition to the colour highlighting, a further central feature of the pictures is the separation of foreground and background: all the tissues not involved in the metamorphosis, which make up the larva's body, are merely drawn schematically. As a result, the action in the plate's foreground is completely detached from events in the background. Finally, there is also the multiplication of the pictures. Isolating an individual organ with the aid of these different pictorial means makes it possible to follow the trail of the changes from one picture to the next. Taken together, the series of pictures evokes the impression of the continuous development of two small red dots into the complex organic structure of the reproductive organs. Herold deliberately employs colour highlighting, the combination of schematic and detailed views, the separation of foreground and background as well as the isolation of a single structure in order to give centre stage to the continuous changes of the reproductive organs.

Metamorphosis as epigenetic development

The reproductive organs were central to understanding the transformation since 'apart from the ability to reproduce [...] the little caterpillar is equipped to perform all the functions of an insect' (Herold 1815: 4). That is to say, the reproductive organs were the only ones which the insect possessed and the caterpillar did not. Herold observed not only how the later reproductive organs emerged from rudiments but also how they changed their location in the course of metamorphosis by migrating further and further down in the caterpillar's body. He thus showed that metamorphosis is an epigenetic transformation. The formation of the reproductive organs from rudiments as well as their migration during development represented a twofold argument for their successive new creation since they meant that the organs were not already present but even replaced other structures whose position they took in the course of development.

Epigenetic development and serial pictures

Swammerdam had still 'extracted' the butterfly from the caterpillar. He had designed a complicated pictorial composition in order to demonstrate the connection between the individual stages on the basis of similar forms. When we come to Herold, however, caterpillars and butterflies no longer have the slightest structural similarity:

> This strange animal, formed out of the egg's liquid and consisting of the stated various parts, has not the slightest similarity with a butterfly. Through the peculiar nature of the organs, of which it is composed during its development, the butterfly is quite dissimilar to the state of its reproductive ability and it thus appears *in the shape of the caterpillar as an independent insect of a peculiar kind*.
>
> (Herold 1815: 4, original emphasis, translation added)

The caterpillar and the butterfly were here two completely different animals. Although they were connected with one another, their connection no longer consisted in having identical structures but a connection through development. Whilst the similarity of structures could be easily depicted and – as in Swammerdam's work – provided an obvious argument for the conformity of the animals, representing a development connection, in which the starting and end points look fundamentally different, required the use of new pictorial means. In Herold's work, this new pictorial technique was the picture series.

The transformation itself was highlighted for the first time in this serial representation. Development was no longer constituted in a single picture but in the relation between the pictures. Organic change was now something which could not be observed itself but which could only be manifested as a series of pictures: the transformation occurred in the pictures as well as between them. Only the sequence of pictures, the interchange of space and representation, fullness and emptiness, depicted and non-depicted, constituted development. It was the sum of changes across the series of pictures which evoked the impression of a continuous progression. But not only development appeared in the picture series. It was more than a mere technique for visual representation. It was a new way of thinking which made it possible not just to depict development connections but first and foremost to conceptualize them.

At virtually the same time as Herold's work, Christian Heinrich Pander's *Contributions to the Developmental History of the Chicken in the Egg* appeared in 1817 and then Karl Ernst von Baer's epoch-making paper *On the Developmental History of Animals* in 1828, with which they laid new foundations for embryology. As with Herold, the serial sequencing of pictures was also key for the concept of epigenetic development in these two fundamental works (Wellmann 2017). The significance of Herold's *Developmental History of Butterflies* for metamorphosis teaching is comparable with the embryological works by Pander and Baer: the change of shape, which metamorphosis described, attained the character of epigenetic transformation. Instead of still designating two opposing forms of development as in Harvey's work, from now on metamorphosis and epigenesis both describe the gradual change of shape, the successive stages of a continuous transmutation in which the organic material repeatedly takes on a new form.

Whilst the picture in the series was constantly repeated, it was never identical to the next picture. Every aspect of the transformation was thus always based on what previously existed, which it continued, but also always changed as it took it forward. As a result, the picture series subjected the continuous change of the organic to a rule, namely the order of repetition and variation. Change therefore followed a rule which it continuously modified without, however, being able to completely break out of this rule. It was only in this alternation between repetition and variation that the concept of development became possible: as a link with the past, which it perpetuated and as a stride into the future, which it opened up. Metamorphosis hence became an epigenetic development and Harvey's distinction finally obsolete.

NOTES

1. From its origins in classical mythology to concepts of modern art, metamorphosis has had a broad impact on art, poetry and culture. Relating this cultural history context to the natural history discussion would be an attractive and rewarding project. For more on the cultural history, see Coelsch-Foisner and Schwarzbauer (2005), Gottwald and Klein (2005), Nicklas (2002), Lichtenstern (1990, 1992) and Barkan (1986).
2. This chapter is a slightly modified and abbreviated translation from the German Wellmann (2008), 'Die Metamorphose der Bilder. Die Verwandlung der Insekten und ihre Darstellung vom Ende des 17. bis zum Anfang des 19. Jahrhunderts', *NTM*, 16, pp. 183–211. Throughout the text, translations from the German and French original are the translator's.
3. Neither a modern history of entomology nor its iconography exist. The standard works, although primarily a collection of material and list of works are Bodenheimer (1928), Essig (1965); on contemporary computational visualization methods, Hall and Martin-Vega (2019); for a history of pests, see Cloudsley-Thompson (1976); and a social history of entomology in the nineteenth century, see England Clark (1995).
4. Thomas Muffet's *Theater of insects* was written towards the end of the sixteenth century. The edition of 1634 appeared with numerous, albeit simple woodcuts. Pictures were also present in the most important works of the seventeenth century. To name a few examples: Malpighi's *Dissertatio epistolica de bombyce* (1669) with the first anatomical depictions of insect larvae; Francesco Redi's main work *Esperienze intorno alla generazione degl'insetti* (1668) or Jan Goedart's *Metamorphosis naturalis insectorum* (1662–69, in Latin 1685). In the eighteenth century, works created in the tradition of physico-theology, such as Johann Leonhard Frisch's *Beschreibung von allerley Insecten in Teutschland* (1720–38) or the

French translation (1742) of Friedrich Christian Lesser's *Insecto-Theologia* were just as richly illustrated as Réaumur's fundamental work, *Mémoires pour servir à l'histoire des insectes* (1734–42). In addition, natural history painters turned their attention to insects at an early stage. The insect pictures by the Belgian painter Jacob Hoefnagel were created in the late sixteenth century. Maria Sibylla Merian, famous to this day for her pictures in the tradition of Dutch still life and flower painting, was active in the late seventeenth century. In Germany, Johann Rösel von Rosenhof und Wilhelm Friedrich Gleichen-Russworm, who worked in Nuremberg in the late eighteenth century, provided not only exact and diverse microscopic observations but also a colourful panorama of the insect world.

5. Swammerdam spent some years towards the end of his life in religious seclusion under the influence of Antionette Bourignon's spiritualist movement. The most important biographical source for Swammerdam is Boerhaave's introduction to the *Bybel der natuure*. The only major monograph on Swammerdam is by Schierbeck (1967); for an introduction also (Cobb 2000). Swammerdam has gained greater attention in the context of modern research into the history of microscopy, see Ruestow (1996, 1985), Wilson (1995), Fournier (1996: 62–72); for further context also, see Roger (1963) and Pinto-Correia (1997).
6. Ruestow places Swammerdam's pictures in the Dutch tradition of miniature painting and anatomy. Giglioni examines the relationship between seeing and microscope, not the connection between picture and metamorphosis, see Ruestow (1996: 132–45) and Giglioni (1998).
7. The terms used in the Latin original are 'mutatio', 'series mutationum' (Swammerdam 1737–38: 2, 3, 4, 6, 11, 18, 42); 'metamorphosis' (Swammerdam 1737–38: 4, 5, 6, 9, 18); also 'transformatio', 'transformatur' (Swammerdam 1737–38: 5, 6, 14, 20). The Dutch terms are 'verandering', 'vervormingen' and 'verwisselingen' (Swammerdam 1737–38: 3, 4, 5, 9, 14, 22).
8. Swammerdam's observation that insects undergo not just one type of metamorphosis as well as its description are still valid today. One basically differentiates between larval stages (development stages with temporary organs which are later shed) and juvenile or developmental forms. These are already largely similar to the adult imagines but do not yet possess any reproductive organs. They only materialise in the course of further moultings from which the imago then emerges. In some insect species there is additionally a pupal stage. If there is no such pupal stage, one speaks of an incomplete (hemimetabolous), otherwise a complete (holometabolous) transformation (in Swammerdam's work the second and third classes, respectively). Insects such as the louse and the flea without any transformation (only moultings after the embryonal stage) as in the case of Swammerdam's first class are designated analogously as ametabolous. This form of development occurs in particular when both larva and imago already populate the same habitat, as is the case e.g. with the locust, see Hüsing (1963).
9. Swammerdam depicted all naturally white insects against a black background and, by contrast, all naturally coloured against a white background, see Swammerdam (1752: 30). In Plates I, XVI and XXXVIII, an additional effect is achieved by representing all vertically arranged pictures as negatives (cf. here Figure 9.1A–D). As a result, they form a kind of gauge along the left picture axis.

10. The interventions of the anatomist are also represented on a few plates, for example in the form of putti (Plate XXIV, Fig. IV) or via the portrayal of the researcher's hands and hand movements (Plate IV, Fig. VIII, Plate XLIX, Figs. V, VI and VIII).
11. What Swammerdam presumably saw with the aid of his preparation techniques are cell clusters, today called imaginal structures or discs. These are subcutaneous invaginations which evolve into organs in the course of metamorphosis; see the current entomological description in Ursprung and Nöthiger (1972). However, these differ from the final shape of the organs so extensively that one cannot speak of rudiments, etc. in the sense of a morphological similarity as Swammerdam postulated.
12. Lyonet was a multi-talented person: lawyer, naturalist and microscopist, draughtsman and engraver; for a while, he also worked for the Dutch diplomatic service as a decipherer of secret correspondence. Furthermore, he assembled one of the most famous collections of shells in the eighteenth century as well as a considerable collection of paintings, see Lyonet (1796). Nevertheless, there is little modern research into Lyonet and his work with the exception of Scholten (2017) and Anthérieu-Yagbasan and Laulan (2021). To this day, the standard works of reference are Hublard (1910), Seters (1962) and Lyonet's anatomical dissections are treated by Cole (1951).
13. The copper plates of Lyonet's first engravings are still preserved in the National Museum in Leiden, see Seters (1962: 68).
14. For more on the copperplate engravings in other people's works, see Hublard (1910: 75–82) and Seters (1962: 65–70).
15. A second edition of the *Traité* appeared in 1762 at the initiative of Lyonet's friend, the physician Le Cat. Unlike the first edition, this also contains an explanation of the drawing boards and a letter to Le Cat in which Lyonet explains his instrument, his magnifying glasses and his anatomical dissections. There is also a plate engraved by Lyonet himself which depicts his instruments (Lyonet 1762: Lettre à Le Cat: 2).
16. This can also be shown by Lyonet's discussion of the anatomy of the head, but there is insufficient room to deal with this here.
17. Lyonet feels compelled to refute possible criticism even in the foreword to his work. On the one hand, he secures his representation on the side of Nature with reference to witnesses ('convaincus par leurs propres Yeux'). On the other hand, he argues on the side of Art that no human being could be as creative as Nature itself (Lyonet 1762: XXIf.).
18. For more on Herold's life, see Runge (1983); on Marburg University, Altpeter (1992); on Herold's work only, Balan (1979: 305–08).

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10

Flow, Attend, Flex: Introducing a Process-Oriented Approach to Live Cell Biological Research

James G. Wakefield

Introduction

The way in which cell biological research is currently undertaken has resulted in hugely valuable advances in our understanding of the fundamental unit of life. The approach itself has evolved via a number of key drivers – historical, societal and technological. It places the highest value on a hypothesis, generating a body of measurable evidence for or against that can be recorded, displayed, analyzed and then shared with a research community, such that the community can then repeat the experiments, reproduce the results and (hopefully) come to consensus. It is commonly assumed that to explore the natural world in this way, the scientist should remove themselves from the biological thing that they are investigating and use as controlled conditions as possible, in order to generate the greatest likelihood of repetition by others. Such objectivity is promoted during a student's education and encouraged during the scientist's apprenticeship (i.e. their MRes or Ph.D.) and the notion of validity underpinning this approach is self-reinforced when it comes to publishing research and applying for funding for further investigations.

A second consideration is that whilst observation of macroscopic organisms, communities and ecosystems maintains a direct relationship between researcher and sample, observation at the level of the cell requires an intermediary – the microscope. The indirect nature of this relationship is further compounded by the way behaviours of live biological samples (be they cellular, tissue or whole organism) are now recorded. Thirty years ago, the researcher would perceive the cell through the eyepiece of the microscope, intuitively taking into account out-of-focus light to maintain the perception of three-dimensionality. In contrast, the sensitivity of contemporary microscopes and the techniques by which live images are now recorded usually requires signal amplification and post-processing. As such, the scientist is observing images many-times removed, on a computer screen.

A further problem with exploring cellular life results from the microscopic scale itself. We see through the diffraction or emission of light from objects, and cells are so small that the diffraction is minimal. Therefore, the vast majority of cell biology uses methods and modes of microscopy that enhance visualization; notably fluorescence (Sanderson et al. 2014). For this reason, the scientist is only able to observe and measure a few features of the cell (membranes, organelles, proteins, etc.) at one time.

Finally, as many microscopes are housed within central facilities that charge for their use by the hour, time is of the essence; thus, researchers tend to engage with sets of images only after the microscopy session has taken place – in research offices that are often shared and subject to distractions. Together, these technical complications and value judgements have resulted in a 'product-oriented' approach to cell biological scientific enquiry and exploration; where researchers are disengaged from the biology they are trying to understand at the point of interaction and where experiments are undertaken quickly, conveyor belt-like, so as to generate the largest amount of data in the smallest amount of time.

And yet, a central human drive is for relationship and active participation. Scientists generally understand that they cannot be removed from the biology they are investigating. Individuals will, if encouraged in an informal, personal setting, attest that a key aspect of the way in which they 'do science' is the exploration of the specimen, an attachment to the associated experience and the use of the imagination to contextualize the phenomenon, in relation to extant knowledge. And although this participation is not formally acknowledged by most, it has been central to some of the advances that have been made; from the relationship between biological form and function in plant development and animal evolution (Goethe in Steiner 2007), to landscapes of developmental biology (Waddington 1957) to the discovery of transposable genetic elements (Fox Keller 1983). However, given the implicit primacy of perceived objectivity and productivity in the pursuit of knowledge, the value of active participation – oriented towards process, and not thing – has not been adequately addressed.

Below are some reflections on developing an active, 'process-oriented' scientific methodology based on 25 years of cell biology research and teaching, stimulated by the work undertaken in collaboration with Gemma Anderson-Tempini and John Dupré on 'drawing the dynamic nature of cell division' and other chapters in this book. Drawing on known the psychological concepts of 'Flow' and 'Flex' (see below) and the ‘delicate empiricism’ of Goethe (1749–1832) (Anderson-Tempini 2017), I suggest ways in which the cultivation of the imagination, intentional creativity and a participatory relationship with microscopic life, applied thoughtfully and validly, can provide new knowledge and insight of the natural world.

An overview of process-oriented cell biological research

If the scientist is going to return to becoming an active participant in an experiment, engaging their intrinsic creativity, it follows that they need to involve their mind as an instrument to explore the cell biological phenomenon or sample. To function optimally, instruments are tuned prior to their use. As such, the suggested process-oriented method involves a preparatory phase, where haptic exercises, rituals, thought experiments and drawing combine in intellectual and physical exercises to focus the mind towards a receptive and maximally productive state of being ‘in the zone’ (‘Flow’). Full engagement can then commence, with particular emphasis on consciously acknowledging the interactions between the internal/living element of the investigation (the biological specimen or phenomenon), the external/mechanical element (e.g. the microscope), the sensory input these provide the scientist with and the interpretation of the input (‘Attend’). A third activity (‘Flex’), occurring either concurrently or after the attending, involves the recollection of prior knowledge, differentiating and integrating information, and intentional switching between different views of matter and energy, purposefully cultivating the imagination and licencing creativity. Finally, by reflecting, repeating and revising these processes, individually and with others, new hypotheses, questions and experiments can be designed and explored (Figure 10.1).

Prior to exploring further the way in which cell biologists undertake their experimental sessions on the microscope, it is pertinent to consider the way in which they approach their interactions with the living biological system in time and space. Currently, interaction is not sought; the traditional method seeks to remove the scientist from active participation and so no value is seen in building such a relationship. Yet the original motivation for wishing to investigate biology, for many, is the sense of awe, reverence and humility that the natural world imbues. For those studying macroscopic phenomena – particularly living organisms in their natural environment – this sense is more easily retained. When investigating the microscopic world, however, the mechanical intermediary required – the microscope – and the local artificial (rather than natural) environment draw the scientist into a transactional relationship with the living cell, tissue or organism. Reminding ourselves that we hold privileged positions as observers and participants of biology, rather than its insensitive masters, allows the scientist to begin their experiment with an open, inquisitive and creative mind.

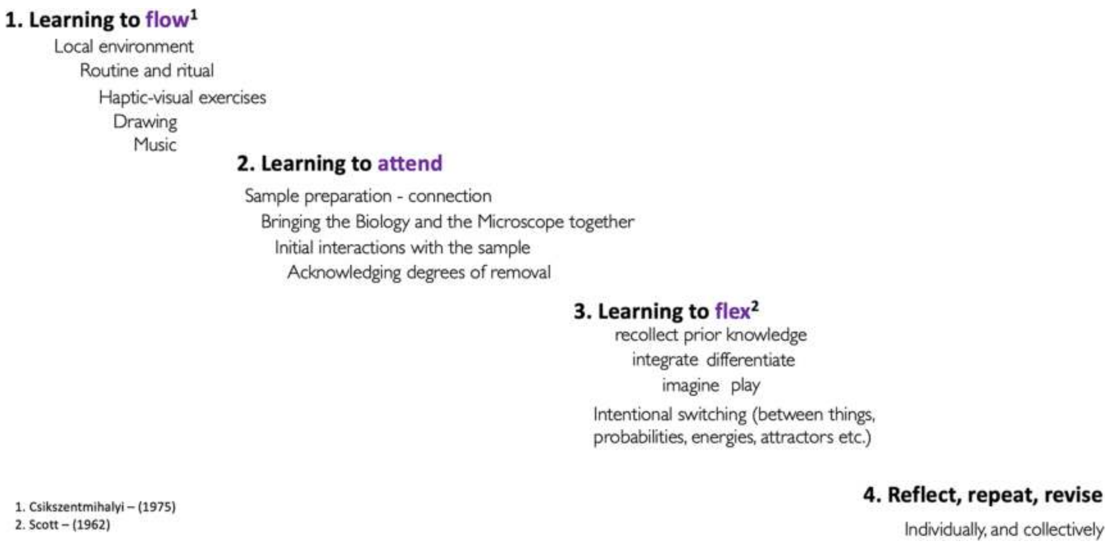

FIGURE 10.1: A flow diagram that summarizes the process-oriented approach in words, subdivided into: Learning to flow; Learning to attend; Learning to flex; and Reflect, repeat, revise. James Wakefield, 2022.

Flow

A wide array of literature exists on the concept of Flow. Initially described and theoretically explained by Mihaly Csikszentmihalyi in 1975, Flow describes the state in which people are so involved in an activity that it feels effortless, with little else mattering (Csikszentmihalyi 1975). As a positive and rewarding mental state, it has been correlated with optimal or enhanced performance in creative fields including sports, gaming/eSports, musical performance and art (Jackson et al. 2001; van Hilvoorde and Pot 2016; Kirschner 2011; Csikszentmihalyi 1996). Although many other focused activities have been linked to Flow (Csikszentmihalyi 1990), the strongest causal links have been investigated in relation to focused, highly skilled visuomotor activities (Harris et al. 2021). Microscopy could arguably be considered a further example of such an activity but, perhaps because the current scientific method holds that objectivity is central, the concept of Flow when undertaking experimental research has not been much explored or described. Interestingly, Csikszentmihalyi himself notes scientific endeavour as a possible recipient of Flow but limits himself to the feelings of achievement in the amateur researcher (Csikszentmihalyi 1990). Yet, from personal experience, I can attest to how being ‘in the zone’ whilst being on the microscope is a frequent and welcome feeling.

Building on the above, below are certain activities which could contribute to an overall state of mind conducive to focused, intense scientific participation:

Attuning to the local environment: As a part of everyday sensory experience, our physical and mental behaviours change as we alter our local environment. Due to the light sensitivity of cell biology experiments, microscopes are usually housed within specially purposed small or partially divided rooms, lacking windows. Thus, as the scientist enters the local environment in which they are going to work, a particular ambience is created. This is generally one of calm and introspection, where the mind can be slowly emptied of distractions. Drawings, words, images and diagrams are all visual cues that can be placed on walls and the surroundings of the room to fill the mental space and can be used on their own or together with short reflections/mediations to enhance concentration, focus and mental clarity.

Routine: Undoubtedly, a part of getting in the zone comes from the practice associated with setting up the microscope for imaging. Taking the protective cover off the microscope, turning on computers, lasers, lamps, checking objectives, starting the imaging software, adjusting the seating are all activities that create a sense of ritual to the experimental session, similar to the 'pre-game routine' espoused in sports Flow. This in turn creates comfort, familiarity and a sense of balance or order which can contribute to clearing the mind, again, preparing it for focused action.

Haptic-visual exercises: One of the greatest barriers to connecting with the biological sample is the 'distance' between the sample and the scientist. Not only does the microscope generate one level of removal but, with the advent of highly sensitive microscopes, the scientist no longer looks down the microscope; instead focusing their attention on the 2D computer screen which represents the sample as pixels of intensity. To reappropriate a perception of three-dimensionality, which can be maintained during the imaging session, handling solid shapes, rotating them and looking at them from different angles can be valuable (Anderson-Tempini 2017). Stimulated by conversations with published work by our collaborator Gemma Anderson-Tempini, we begin in our lab with a set of wooden Platonic solids. These 'idealized', regular forms emphasize not only three-dimensionality of physical objects but also symmetry/asymmetry within a form. If possible, this exercise can be followed by a similar one using a 3D printed version of the biological sample being studied; such shapes can be generated using experimental datasets. It may also be beneficial to view 3D or 4D (3D over time) image sets from previous experiments, or from artistic interpretations of the biological processes (such as the representation of mitosis described in 'drawing the dynamic nature of cell division' [Anderson-Tempini et al. 2019]).

Drawing exercises: In concert with the haptic exercise, drawing can be a powerful focusing method prior to imaging. Drawing familiar biologically relevant shapes, structures or representations of processes all positively reinforce the expectations of the scientist but allow imagination and creativity to enter the preparatory activity. The value of this approach has been ably demonstrated in our previous work (Anderson-Tempini et al. 2019) and in the other chapters of this book.

Music: Although we have noted the intrinsically quiet surroundings of the microscopy room, it is worth considering whether music can be used as an asset. The connection between music and Flow has been noted for over 30 years (Csikszentmihalyi 1990), and certain types of music have been demonstrated to both increase focus (Sridharan et al. 2007) and to elicit activity in the reward centre of the brain (Gold et al. 2019). As such, health and safety guidelines permitting, playing of certain types of music prior to and during imaging may be beneficial in triggering the Flow state.

Together the above exercises, many of which are simple adjustments in consciousness and additions to existing practice could dramatically enhance focus on the task at hand – the dynamic interaction between scientist and biological phenomenon – promoting the Flow state that correlates with optimal performance.

Attend

The eighteenth–nineteenth-century German poet, writer and scientist, Johann Wolfgang von Goethe, expounded a dynamic view of natural phenomena that is implicitly process-driven and that can be explored and understood through connecting isolated pieces of knowledge. Although much mis-interpreted and dismissed, both in his time and since, his approach led to a number of scientific breakthroughs, including in the fields of animal evolution (the ‘discovery’ of the human intermaxillary bone) and plant developmental biology (the *Urpeflanze*) (see Craig Holdrege for review). The essence of his approach was a ‘delicate empiricism’, creating connection with the biological phenomenon being studied, careful observation, qualitative identification of variations of form or function, repetition and recognition that a single example is reflective of a universality and vice versa (Anderson-Tempini 2017). Perhaps the most relevant centrality of Goethe’s methodology was the concept of the ‘*aperçu*’.

> An *aperçu* is a special insight: a directed synthesis that allows us to anticipate a whole or a totality by means of a particular instance. As anticipatory, *aperçus* need substantiation. They are not given as simply true; they can be hypothetical, *problematic or*

> *even false*. Moreover, *aperçus* are dynamic. They are like conceptual engines that propel a way of seeing and imagining.
>
> (Sepper 2009)

Such attending to detail in relation to a particular specimen, whilst holding in mind its relationships with other specimens of the same type, or lower/higher organizational levels is, to some extent, subconsciously practiced by cell and developmental biologists. However, references to drawing this practice into the light and intentionally applying it specifically to the study of the microscopic are few. Researchers often forget just how much knowledge and understanding they possess. In relation to cell biology, where specialized and expensive technology is required, within a relatively short space of time an individual can accumulate more experience of a particular natural phenomenon explored within a particular set of conditions than anyone else in the world. Yet, for the most part, we treat this privilege far too lightly. Instead of giving it our full attention each time we observe it, the automated nature of capturing the phenomenon through camera, photomultiplier tube and screen means that the researcher's focus can often be elsewhere while life is unfolding in their absence.

To fully attend to a process is to engage with it, acknowledging its presence and the interaction that develops between the observed and the observer. Although, as previously noted, the necessity of intermediators – first the microscope and then the detector/computer – separates the phenomenon and the scientist, there are opportunities to forge a relationship which can add value to the scientific process.

Sample preparation: The initial interaction with the microscopic sample usually occurs just prior to imaging, when the specimen is transferred onto a microscope slide/coverslip to the objective lens. This may be direct, as is the case for tissue culture cells grown on the coverslip itself, or it may require a series of steps where the sample is manipulated, for example when tissues are isolated, or embryos 'mounted'. These manipulations are skilful and dextrous procedures using living organisms. Although learning such procedures requires concentration, repetition of them by the experienced scientist who may have carried them out hundreds of times can render this process unmindful. It is therefore useful to bring attention back to the nature of the interaction – a dynamic relationship between two living entities. One suggestion to achieve this is to again use visual cues (pictures, diagrams and photos) on the walls of the microscope room, such that the scientist consciously re-familiarizes themselves with the process and specimen being studied and its dynamic, living nature, while attempting to visualize the process in three dimensions, over time.

Bringing the biology and microscope together: The point at which the internal/living element of the investigation (the biological specimen) will be combined with the external/mechanical element (the microscope) should again be consciously acknowledged by the scientist. This tool – the microscope – provides the opportunity to visualize processes not normally discernible by the human eye but removes the observer into an indirect relationship with the sample. Again, ritualistic manipulations, such as movement of the sample coverslip onto the microscope stage, change of objective lens, addition of immersion oil to the sample/objective and switching of controls from eyepiece to camera and back again, all provide opportunities to re-affirm 'the zone' of concentrated enquiry.

Building a relationship with the biological sample or phenomenon: The observer will need to begin enquiry with an assessment of the overall 'health' of the living sample. This 'quality control' step ensures that the observations being made are not an artifact of sample preparation, but truly reflect the biological sample/phenomenon as revealed by the scientific experimental conditions being studied. These initial interactions are often made using brightfield (white light) illumination and, again, the trained observer will usually undertake a brief analysis, almost subconsciously. To bring this to the conscious fore, referencing to key qualities, such as tonality, symmetry, regularity and texture, written up and placed within the wider field of view can be used.

Acknowledging secondary degrees of removal: The transition to sensitive imaging of sub-cellular structures and processes requires the transformation of information from a secondary interaction (sample to microscope to eye) to a further removed one (e.g. sample to microscope to detector to amplifier to processor to screen to eye). For many microscopes, it also requires the accumulation of information in 2D planes rather than the pseudo-3D that the human eye recapitulates when looking down a microscope eyepiece. The researcher therefore moves from a holistic to a more specific interaction with the phenomenon. As such, it is beneficial to again acknowledge and attend to this removal, imagining these different levels of removal and the relationship between what is observed and what has occurred for the observation to take place.

The main session: Prior to the development of highly sensitive cameras and detectors linked to recording devices (i.e. computers), the scientist would be required to record and document the cell biological phenomenon concurrently with the observation through drawing, annotation and notes. The exquisite detailed drawings of cell division, published by Walther Flemming in the 1880s, the ideas, hypotheses and understanding they contributed towards and their similarity to the images captured on advanced microscopes attests to the value of such an approach (Anderson-Tempini et al. 2019). Now, however, the major aim of the microscopy sessions is to generate 'output' – 2D and 3D sets of time-lapse images that are further modified and analyzed at a later timepoint using analysis software, such as Fiji/ImageJ (https://imagej.net/software/fiji/).

Quantitative image analysis is undoubtedly hugely valuable – automated measurement of parameters of interest using these tools provides robust data without human error or bias. However, by relegating the exploration of the phenomenon to, sometimes brief, post-hoc analysis sessions in shared research offices, the dynamic process of interaction with the living cell is lost. Remaining connected to the phenomenon while it is actually taking place allows for continued physical and intellectual input and analysis on the part of the scientist. Drawing the process as it unfolds serves to focus the attention to detail, providing opportunities for imagination to flourish; for example, consciously recognizing that the images being generated reflect only one or two physical elements of the process, in amongst the many thousands, helping us to place our observations and analyses within a wider, holistic context.

Unlike the preparatory phase of a process-oriented methodology – which undoubtedly requires additional time in relation to existing practice – the techniques described above are, in many ways, actually a wiser and more judicious use of time than is currently undertaken. Instead of pressing a recording button and becoming distracted by other unrelated tasks (reading, writing, phone checking, etc.) or even leaving the room, they provide a connection to the living sample and opportunities for cognitive flexibility (see below).

Flex

When a scientist approaches a biological phenomenon, they do so with a particular mind-set in relation to what they consider to be important contexts. This, in turn, colours the questions that are asked, the way in which they are addressed and the interpretation of the results of experiments. The exclusivity of things-based science (atomism, reductionism) as a valid approach is ingrained into the way in which biologists approach their hypotheses, experiments, analyses and conclusions. A process-oriented scientific methodology requires the scientist to think differently. The suggestion here is not that one or the other has exclusivity in cell biological research but that different ways of thinking, and the conscious switching away from a things-based worldview, can result in new knowledge and understanding. In many ways, this switching of emphasis of thought can be compared to cognitive flexibility (Flex) – a now broad term used in behavioural psychology (e.g. Magnusson and Brim 2014; Buttelmann and Karbach 2017; Uddin 2021). In its original context, Flex is defined as 'the readiness with which the person's concept system changes in response to appropriate (environmental) stimuli' and is measured in relation to cognitive complexity – 'the number of independent dimensions-worth of concepts the individual brings to bear in describing a particular domain of phenomena'

(Scott 1962: 405). It refers to the ability to near-simultaneously consider multiple aspects of thought, switching between 'characteristics such as differentiation, integration, rigidity, flexibility, and so forth' (Scott 1962: 405). As a set of thought processes, Flex can be practiced either during the microscopy session itself, as the relationship between the observer and the observed is being built, or during a post-hoc analysis session. In either case, it involves combining prior knowledge of the expert and the experience/information of the new data with imagination.

Switching between thing and process

Many cell biological studies are portrayed as understanding 'the function of the gene' (or the protein encoded by the gene), after its removal (i.e. 'knocking out' or 'knocking down' the gene, using mutation or RNA interference). Hence, the focus of reductionist studies on the 'parts'. A complementary (and, it can be argued, more accurate) description of the altered phenomenon is that it demonstrates the way in which 'cell processes and behaviour are altered' as a consequence of loss of a protein. This may appear to be a subtle distinction. But it is significant. In the former, interpretation focuses exclusively on the thing (i.e. the gene or gene product). The mind is drawn to it, usually in the context of a cog within a (albeit complicated) mechanism and the conclusion is drawn that 'this' gene is required for 'that' process. In the latter, the 'agency is flipped' and the system is paramount. The mind is drawn to the phenomenon and its dynamic responses, re-calibrations, activities and altered attractor states when it is perturbed through loss of 'that' gene product. The information itself (the measurement or description of the way the biological phenomenon changes upon loss of a protein) does not change, but the perception of what is important in the mind of the scientist does. In many ways, intentional switching between emphasis on the parts and the process is what Goethe routinely practiced: 'I regard all phenomena as independent of one another and seek to isolate them at whatever cost; then I regard them as correlates, and they connect up in a decisive vital whole' (von Goethe and Naydler 1996: 57). And yet although we have a framework (standard scientific enquiry) that reifies reductionism and differentiation of phenomena, similar conceptual engines (*aperçus*) for processes and synthesis of phenomena are open to the imagination.

Imagining the process

Harnessing the imagination to investigate the living world, in one sense, comes naturally to the scientist. Synthesis of prior and new knowledge stimulates ideas as to how it 'might actually be' – ideas that lead to hypotheses that can be tested.

But, in the same way that acknowledging the participatory relationship between phenomena/sample and scientist is left unacknowledged, the role of intellectual creativity in scientific endeavour is likewise played down. The focus of my laboratory's research is the formation of the mitotic spindle. In 'thing' terms, the mitotic spindle is a bipolar sub-cellular structure composed of many thousands of dynamic protein filaments (microtubules) that exert force on duplicated chromosomes, allowing them to align in the centre of the spindle and segregating them equally to facilitate cell division. Below are just a few closely related, but distinct, *aperçus* that can be harnessed to focus on spindle formation as a process:

Energy landscapes – At first glance, any talk of energy landscapes within science is likely to result in calls of 'pseudo-science' or 'flakiness'. However, it was precisely the conception of a shape/profile of sub-cellular energy bodies that led to our recent new representation of cell division (Anderson-Tempini et al. 2019). Rather than concentrating on the individual molecules or structures that generate the force required for chromosome segregation, we imagined the force exerted by the spindle itself, holistically without space, but within time. This led to a series of biologically relevant questions about how energy is created, used and dissipated during this fundamental biological process.

Statistical likelihoods – The dynamic nature of cell biological processes can be thought of as changes in activities over space and time. It can be helpful to conceptualize this in a probabilistic sense. Imagine a tree, exposed to the wind, comparing one moment in time with the next. The space filled by the trunk will not change – its mass is immovable to the force of the wind. Its branches, however, will sway – in any one future moment in time, they will fill a slightly different set of *x*/*y*/*z* co-ordinates. In this *aperçu*, the bulk that constitutes the leaves will be a 'buzz' – there will be a probability that, say, 90 per cent of the leaves will fill 90 per cent of the same space, but as you move towards the edge of the mass of leaves, the likelihoods decrease. A similar representation of space/time likelihoods can be fruitfully employed with spindle formation. Here, a distinct imagining of the differences in 'solidity' of the centre and the edges of the spindle occurs and the mind is drawn towards understanding the dynamics present at those edges.

Attractors – In the dynamical systems theory, an attractor is a set of states or physical properties towards which a system tends. A symmetrical, self-organizing mitotic spindle, where the central attractor is bipolarity, provides a different *aperçu* to either of those described above. Now, the mind is drawn to the dynamic tension between the basin of attraction – the tendency towards a stable bipolarity – and the necessary responsive, dynamic pull away from stability that allows microtubules to explore physical space over time.

Doing process biology is a process

Implicit in the discussions above is the time it takes to cultivate a process-directed scientific methodology alongside a more traditional mode of doing science. The reflective, imaginative process of Flex is stimulated by concentrated attending to the process being explored, which is itself made fruitful by Flow. Nor does the cultivation come to fruition immediately, through a single session – or by a single person. Iterations – reflection, repetition, revision – are familiar concepts in traditional scientific approaches and no less valid here. Similarly, sharing imaginative time with colleagues, asking each other questions, trying to imagine the dynamics of the phenomenon being explored through drawing labs (see Chapter 9) and other means is far more productive than working independently. It took many such interactions over many months, with input from a philosopher, artist and several scientists to begin to conceptualize our new representation of cell division.

A key question will undoubtedly be – is it worth it? When publishers, faculty positions and progression are calling, is it not better to push on with a tried and tested method of generating data? Perhaps if they were the only 'attractors' to scientists. But there are reasons why a process-directed scientific methodology should be championed. First, for many, the ego and the money are secondary to the awe and wonder of the natural world and the curiosity and drive to do what we can to explore it. Embracing the feelings underpinning the doing of science is to recognize the humanity within the process. In a world where happiness and fulfilment are increasingly being seen as integral to our jobs, acknowledging the joy of creativity within science can have a positive impact on wellbeing in the workplace. Second, as argued above, and elsewhere in this book, process biology is a complementary framework to the standard objective approach. The conceptual frameworks and the questions being asked as a consequence of permitting the imagination into scientific practice contribute new ideas, hypotheses and knowledge of the natural world. It may seem premature to compare the results of process-directed methods with those of the traditional objective approach in cell biology and beyond, but this does not invalidate the evidence that has already accumulated. Doing process cell biology is a process – and one that needs exploring.

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Process Epistemologies for the Careful Interplay of Art and Biology: An Afterword

Sarah R. Gilbert and Scott F. Gilbert

A book – like an organism, like an artwork – is always more than the sum of its parts. As a gathering of practices dispersed across the too often-siloed fields of art, science and philosophy, this book offers a rare opportunity to un-discipline urgent questions around changing life. This is not to say that disciplinary assumptions and methodologies are absent. Quite to the contrary, the included papers explore a wide range of what Haraway (1988) calls 'situated knowledges': explicitly partial perspectives that allow us to become accountable to each other for how we learn. Notably, each practitioner in this volume brings not only their own bundle of situated expertise and skills but also a commitment to loosening or even undoing, some of the disciplinary strictures and other habits of thought that often constrain thinking across divergent practices. Put simply, the participants of this project came to play, eager to learn from the unexpected affiliations and generative frictions of this encounter.

When Gemma and John invited us to reflect on, amplify and interact with these thought-provoking contributions, we were happy to join the party. The time was certainly ripe for such a symposium, as ideas of the process have created new priorities in the field of biology and its visual representations. The result is a book that asks us to follow various problems and practices as they move betwixt the unstable territories of what we casually call 'Science', 'Art' and 'Philosophy' – hardly settled and uniform fields, but rather shifting sets of heterogeneous practices tending to cluster around different modes of thought.

Different modes of thought are important because they allow different kinds of problems and questions to become intelligible. It has been said many times, but it bears repeating (from the rooftops!): we are not interested in one true epistemology to rule over all others. We must instead work to aid in the survival and proliferation of specifically situated knowledge practices. Thinking about life's processes alongside practitioners in this book and beyond, we aim to draw out disparate threads of particular 'stickiness', resisting the tendency to collapse difference into an agreement or, in Haraway's terms, to equate thinking with the 'dispelling of trouble' (Haraway 2016). Far from undermining Art/Science collaborations, we hope that these nagging threads, if pulled hard enough or in relevant directions, might do some useful work in helping to unravel the still persistent myth of C. P. Snow's 'two cultures' (Snow 1959) and the tired battles still being fought over each culture's claim to epistemological superiority. Supporting instead what Isabelle Stengers (2017) calls 'an ecology of practices', we write here collaboratively, as practitioners of different crafts (in the most general terms of sculpture and biology, respectively) with 'an active sense of the positive partiality of our practice[s]'.

Changing biology by changing drawing/changing drawing by changing biology

In his analysis of Cézanne's drawings, art critic Peter Schjeldahl (2021) has written about 'the timeless purpose – and the impossibility – of pictorial art: to reduce three dimensions to two'. How much greater, then, is the impossibility of reducing four biological dimensions (the fourth being time) to a two-dimensional space? John Dupré brings to the discussion the concept of process biology, both in its ontology and epistemology, emphasizing that biological entities can be seen as processes as well as objects. Until recently, biology has centred around organisms, organ systems, their cells and their genes. So it is not surprising that scientific drawing has focused on the attempt to represent entities, not processes. Such drawing skills used to be part of the biological curriculum, and biologists had been instructed that if you haven't drawn it, you haven't seen it (Root-Bernstein and Root-Bernstein 1999; Gilbert and Faber 1996).

In biological illustration, there are, perhaps, four major perspectives, four modes of relationships into which living beings are placed: the mode of a predator, the mode of a connoisseur, the mode of an abstractionist and the mode of a romantic. Each is needed, and each is incomplete. The 'predatory mode' is highly developed in the naturalist, and it is the ability to spot a salamander camouflaged in the soil or a butterfly on a vine. The 'connoisseur's mode' is the ability that can look at a thrip and identify its family from the shape of its tenth abdominal segment. This mode of viewing life is often highly developed in professional biologists.

Both predatory and connoisseurial perspectives are important in biology. Darwin had the predatory eye of a naturalist, honed by years of collecting beetles in the fens of England. He also had a connoisseur's eye, but only for barnacles. He didn't recognize, for instance, that the birds he had collected in the Galapagos were all finches. The bird expert, the ornithologist/artist John Gould, had to tell him that. The realistic representations of turtles in art, textbooks and monographs provide another example of both types of eyes. David Carroll, for instance, has a trained naturalist's eye that can recognize a turtle on the banks of a sandbar laying her eggs in the late evening. For Carroll, who consciously calls his contributions 'natural history', context is critical (Carroll 1996), and his turtles are represented in their respective environments. His turtles are always doing something.

For Louis Agassiz, the critically important Harvard biologist of the late nineteenth century, turtles were drawn only after the turtle was removed from its environment and brought into his laboratory. Agassiz's book on turtle embryology is a classic, and one of the most beautifully illustrated biological monographs ever published (Agassiz 1857). However, it is a museum offering. The stages of turtle development are not in a linear sequence. Adult and embryonic stages are placed alongside one another in frames, and one can imagine oneself looking down at a museum drawer, where the specimens are laid out for your viewing. Agassiz was the prime museum enthusiast in America (Winsor 1979; Lurie 1988), and the full name for the MCZ had long been 'The Louis Agassiz Museum of Comparative Zoology'.[1] The Museum opened in 1859, two years after the turtle volume. Indeed, the turtle volume can be considered as an extension of Agassiz's new museum.

Agassiz helped change biology by changing the way turtles were represented. Agassiz was branding himself as a 'scientist', and as Laura Dassow Walls has shown, he and other scientists were becoming 'modern' through their separation from nature and their ability to stand above it (Walls 1997). He denigrated 'natural history', relegating field biology to a second-rate status suitable for amateurs (Tauber 2001). Agassiz was himself an artist who taught his students to draw specimens, but they were dead specimens in a classroom dish or a laboratory pan, not in a pond or stream. Walls notes that Agassiz praised natural history in his act of 'purifying' it.

> But while Humboldt enacted his method in the chaotic conditions of the field, Agassiz enacts the Humboldtian method in the vacuum of the laboratory, thereby gaining precision and control. Agassiz both honored his mentor's name and warned against imitating him.
>
> (Walls 1997: 24)

The 'epistemic virtue' (Daston and Galison 2010) of animals being represented in context is being replaced by one of precise isolated objectivity. Agassiz trained his students for connoisseurship, and many were awarded choice positions in American universities.

In other words, the manner of drawing – the detachment of the organism from its environment – helped create a manner of science. And that type of science promoted that manner of drawing. By drawing specimens out of their context and individuated, Agassiz had used drawing to reframe organisms, taking them out of natural history and into a 'modern' science. This is an important lesson for those seeking a similar revolution in biology today, promoted in part, by its art.

We also see this symbiosis of science and drawing in the study of insect metamorphosis. Janina Wellman, in this current volume, shows that while K. E. von Baer and H. Rathke helped free the study of vertebrate development from the paradigm of preformationism, Johann M. D. Herold was showing epigenesis (and not preformationism) in insects. While Pander and von Baer observed germ layers and guts to establish that organisms formed their organs anew each generation, Herold looked at the generative organs of butterflies and produced panels of drawings to show their gradual developmental changes. This way of showing process has become normative in embryology texts. Here, too, a change in drawing style accompanied the change in biological paradigm.

But to draw a biology of processes, one needs to have the 'abstractionist' mode to imagine the process as an entity, itself. The naturalist painter Maria Sybilla Merian may have drawn the first abstractionist renderings of life (Merian 1705; Todd 2007; Nutting 2011). Here, again, insect metamorphosis was used as an exemplary process. Though her lithographs included realistic depictions of nature, she arranged the drawings of eggs, larvae, pupae and adults to show an abstract process, the insect life cycle, something never before depicted. The egg (and the plant upon which it was laid), the larva (eating that plant), the pupa and the adult butterfly were all on the same page, creating something new – the life cycle. Taking science to a new level, emphasizing life cycles and interspecies relationships, she also changed the art. Botanical images of her period had favoured grid-like treatments, emphasizing similarities (Jardine et al. 1996: 101; Reitsma 2008: 209). Merian's portrayal of nature reflected the vibrant and varied environments of the South American tropics.

The abstractionist mode was first recognized by diachronic biologist Conrad Hal Waddington (1968), who felt that in the twentieth century, both art and science had tried to get 'beyond appearances'. This led to movements towards abstractions in both art and biology (where genetics provided a look 'beyond' the phenotype). The abstractive view can be seen in the Watson and Crick models of the double helix and in Jane Richardson's drawings of protein structure. These semi-diagrammatic representations remove the physicality from the molecules and just show the framework that gives the molecule its functions.

John Dupré has emphasized that life is sustained predominantly by three processes: metabolism, the life cycle and symbiosis. Metabolism is nothing less than the ability of an organism to retain its identity by changing its parts (Jonas 1966). It is one of the major ways of characterizing life. When it comes to the life cycle, one of the most influential process biologists has been John Tyler Bonner. Whereas even process philosophers such as John Dupré will say that 'organisms have life cycles'. Bonner (Bonner 1965; Gilbert 2019) postulated that organisms *are* life cycles. Indeed, seeing things this way – the body as part of the life cycle process – allows one to see (as Dupré has suggested in his talk) that Boris Johnson is both egg and prime minister. Symbiosis is shown as the third process of life, and all animals share the property of being both organisms and ecosystems. We are holobionts – consortia of numerous species integrated into our physiology, immunity and development (Gilbert et al. 2012; McFall-Ngai et al. 2013). But as biology becomes a science of processes, of becoming (see Gilbert and Epel 2015; Nicholson and Dupré 2018; Fusco 2019), it demands a different mode of drawing. Perhaps, it needs a 'romantic mode', a perspective that uses intuition to connect processes that had been considered distinct.

Indeed, Figure A.1A is a figure that one of the authors of this essay (S. F. Gilbert) is commissioning for the next edition of his developmental biology textbook. Here, symbiotic bacteria are necessary for the life cycle of the sponge *Amphimedon*. A metabolic cycle, a life cycle and symbiosis are integrated into a common scheme. The bacterial symbionts make the chemical compounds needed for the sponge larvae to synthesize nitric oxide (NO), the chemical signal necessary for initiating their metamorphosis. The symbiotic life cycle allowing the turning of the host life cycle is a diagrammatic scheme that had been drawn for a previous paper (Figure A.1B).

Drawing a biology of process has had its proponents and even some remarkable examples. Waddington's epigenetic landscape (as described and interpreted by two chapters in this volume) is an amazing epistemological illustration (Squier 2017). Even Charles Darwin's 'tree of life' can be seen as a diagram that represents processes. Darwin thought so, saying that just as new life arises in the buds of trees, so new life emerges from existing life forms, the green and budding twigs representing existing species (Darwin 1859). Moreover, even *processes* have homologies and isomorphologies (*qua* Anderson-Tempini) with other processes. One of these is evolution. Even before Darwin had popularized his famous sketch of the bifurcating lineages of animals, August Schleicher had proposed a *Stammbaumtheorie* of language evolution and had drawn trees showing the bifurcation of Indo-German languages (Schleicher 1853). Tree diagrams have also been used to show the evolution of religions (Gilbert 2003), and are similarly based on documentary evidence, homologies and the retention of unused structures. Similarities in developmental

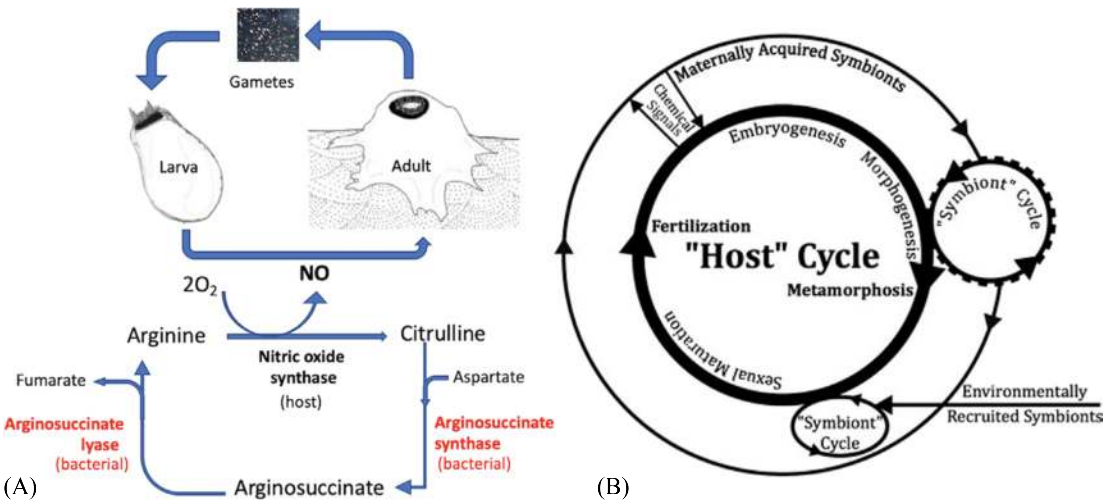


FIGURE A.1A and B: Holobiont life cycles. (A) A sketch integrating the life cycles of the sponge *Amphimedon* and its bacterial symbionts (modified from Song et al. 2021). Note the arrows designating the life cycle processes (above) are merged with the arrows denoting the biochemical processes (below). (B) A conceptual diagram for integrated host and symbiont life cycles (drawn by David Gilbert and published in Gilbert 2017).

processes have shown that the pathway by which segments form in *Drosophila* is isomorphic to the pathway by which the anterior–posterior axis forms in the roundworm, the dorsal–ventral axis forms in frogs and the initiation of certain cancers in humans (Gilbert and Bolker 2001; DiFrisco and Jaeger 2021).

Hence, not only can genes, cells and organs be considered homologous but so can processes. Not even the gene is outside of flux. The DNA gets renewed at each cycle of replication, and what DNA is a 'gene' is a matter of cellular interpretation (Stotz et al. 2006; Stamatoyannopoulos 2012). Seeing life as an evolving set of processes, including metabolism, life cycles and symbioses, is a way of seeing life wherein the organism, the cell and the genome are in flux and whose component parts are entities that are made through the concrescences of numerous processes. Perhaps a more appropriate name for Gaea would be that of her Titanic daughter, Rhea, 'she who flows'.

Drawing as a partnership to liberate both scientists and artists

If scientists now know that what we call 'organism' and 'environment' are actually inextricably enmeshed as a process of continual and contingent co-construction, then why do so many of us still tend to feel like those all-too-human individual organisms? If heterogeneity and flux are fundamental to our very biological functioning, why don't we experience these sensations more consistently, as elemental throughout everyday life?

Turning to aesthetics, we might begin by reorientating towards questions of the sensible and 'the power that inhabits the sensible prior to thought' (Ranciere and Djordjevic 2004: 2). For the French philosopher Giles Deleuze, thought, in its proper sense, cannot be individually conceived of or represented, because it does not emanate from, or belong to, any single subject. Emerging relationally in all the fleeting contingencies of lived experience, it can only be *sensed* or *felt* (Deleuze 1968/1994). This distinctly *asubjective* approach to sensation and relational thinking invites us to consider the many fecund sites of potential co-construction we might be overlooking (and neglecting to nurture) in our deep-rooted presumptions around individual agency and autonomous subjectivity.

Indeed, Kant's Copernican revolution in thought made subjectivity 'logically compatible' with scientific reason *precisely* by rendering questions of feeling irrelevant or, at the very least, an afterthought: before all else, subjectivity was presumed to be rational, structuring and ordering the world prior to our experience of it. What we lost, in what Whitehead calls this 'bifurcation of nature' (1920), is nothing less (and quite a bit more) than what aesthetics, as distinct power of thought, aims to recentre: rich worlds of affective potentialities epistemologically devalued and left unexamined, simply for want of being measurable or otherwise directly accounted for by known physical laws. For practitioners committed to the study of changing life, (re)opening the sensible as a legitimate site of epistemological inquiry could hardly be more urgent.

'The release from scientific restraints in artistic practice', say Anderson-Tempini and colleagues in this volume, 'makes collaborative image-making an open-minded experience that can be mutually beneficial for scientist and artist alike'. She and the Wakefield laboratory scored the orchestration and choreography of mitosis in several different types of cells, linking intuitive feelings and quantitative data. Musical metaphors, including that of dance, have been used to describe cell biology before (e.g. Gilbert and Bard 2014; Noble 2016), but this was probably the first time they were taken seriously enough to actually make a physical model of a physical cellular process. The changing amounts of energy dedicated to each process determined the shape of the vessel at any moment. The 'final' result, 'Garden of Forking Paths. Mitosis Score no. 5', shows mitosis *as* the cell, where the processes *are* the parts. As Yeats (1929) asked, 'How can we tell the dancer from the dance?'

There were calls and responses, and mutual inductions where exchanges were made between the drawings, the artist and the scientists. Imagination was added to the data and to the conventional imagery. As the artist and scientist found ways to represent processes, the diagrams generated new questions involving the relationship of energy to mitosis. The drawing and verb-making exercises slowed down the science and gave scientists the opportunities to think about what they did not know. Drawing is seen as a technique of liberation. James Wakefield has likened it to slow food, echoing Isabelle Stengers's idea of 'slow science' (Stengers 2018). Slow science, like slow food, he notes, takes time, care and relationships.

But from what are they liberating scientists? The enslaver, according to Waddington (1977), is an overarching fiend called COWDUNG. This is an acronym for the Conventional Wisdom of the Dominant Group. Its power comes from its being the source of funding, prestige and employment. So, as John Dupré remarked in the symposium talks, one must be very wary in one's dealings if you have evidence against it. COWDUNG holds that the arts (and artists) are peripheral (if not harmful) to science,[2] that reductionism is the sole ontology and epistemology of science, and that having fine motor skills is unimportant to their scientific inquiry (Root-Bernstein and Root-Bernstein 2013; Hill 2018).

COWDUNG also defines the boundaries of what is professionally acceptable, and as Anderson-Tempini noted, partnerships between artists and scientists are a way of liberating both the scientist and the artist from such conventions. Such collaborations have indeed been helpful in giving scientists new perspectives, outside their established terrain, and they have also allowed artists to see things never before depicted. Agassiz, for instance, was wealthy enough to afford the services of a cadre of artists such as Henry James Clark and August Sonrel (Blum 1993).[3] The drawings of microscopic turtle embryos show parts of the turtle's developmental anatomy (such as the carapacial ridge that initiates shell development in the dorsal dermis) that were only named in the 1980s (Burke 1989).

Perhaps even more fruitful for science was the partnership of biologist Christian Heinrich Pander and artist Eduard d'Alton. Although Pander is often credited with the discovery of the three germ layers of the early vertebrate embryo – the ectoderm, mesoderm and endoderm – it was his artist, d'Alton, who first visualized and meticulously drew these as-yet-unnamed structures. Pander's embryology of the chick was the best done to that date and d'Alton's drawings were critical in making it so important (Wessel 2010). Historian Frederick Churchill (1991: 4) has noted the 'mismatch between that which Pander covered in his account and that which d'Alton illustrated'. Whereas Pander gave a rough description of heart development, d'Alton deftly portrayed the chambers of the heart, the three aortic arches, the sinus venosus and the fusion of the dorsal aorta. d'Alton also drew the incipient brain bulges that we now know to be the telencephalon, diencephalon and mesencephalon. Pander did not comment on these regions nor did he recognize their distinctions; but the artist saw them to be distinctly present. Priority of discovery of the aortic arches and brain vesicles might better be given to the artist who saw them rather than to the later scientists who named them. From Pander and d'Alton onward, Churchill concludes that embryology was to become heavily dependent on its pictorial representations.

Another remarkable collaboration showed the interactions of microtubules and chromosomes during cell division, the processes that were modelled by Anderson-Tempini. These processes were gloriously revealed in the book that brought photography into embryological illustration, *An Atlas of Fertilization and Karyokinesis of the Ovum* (1895). These photographs were the collaboration of developmental biologist E. B. Wilson and photographer Edward Leaming (Wilson and Leaming 1895). Noting that van Beneden and Neyt had published photographs of roundworm embryos, Wilson claimed that Leaming's photographs were far superior since they were from his microscopic sections, rather than from wholemounts. By photographing thin sections of sea urchin eggs, Wilson and Leaming were able to show the interactions of the chromosomes with protein fibres (the microtubules) during fertilization and mitosis. In addition to these photographs, Wilson placed camera lucida drawings of the same slide as the photograph to provide labels and explanatory captions (Figure A.2). In his preface, Wilson notes that knowledge of fertilization and cell division must 'be acquired from text-books in which drawings are made to take the place of the real object'. He quickly adds, however, 'But no drawing however excellent can convey an accurate mental picture of the real object'. And while the best drawing 'embodies a considerable amount of interpretation', the photograph at least gives 'an absolutely unbiased representation of what appears under the microscope'. There are faults with photographs, to be sure, but 'they are faults of omission rather than commission'. In his 'Note on Photographic Technique', Leaming mentioned explicitly that no retouching of the plates was performed. It was in this book that DNA was proposed as the physical carrier of inheritance and that the endoplasmic reticulum was seen to join the nuclear envelope to the cell membrane. A year later, Wilson would use such

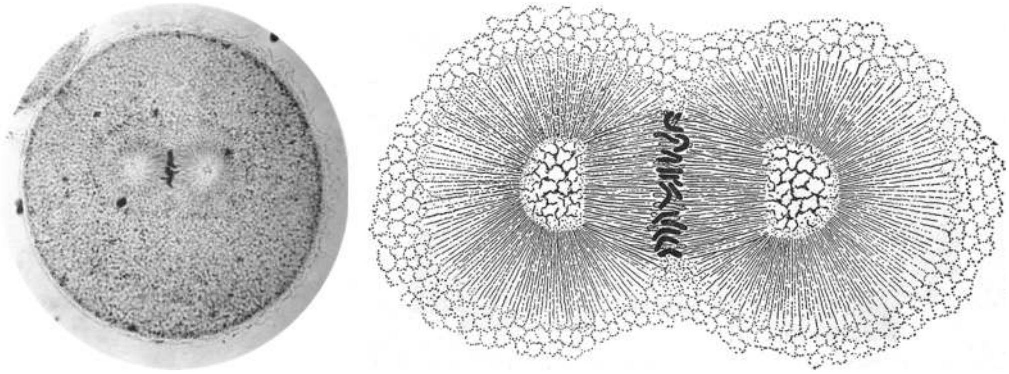


FIGURE A.2: Phototype 26 (left) of Wilson and Leaming (1895) with its accompanying diagram (right), showing the chromosomes of sea urchin zygote forming an equatorial plate in the centre of the cell. The 'astral rays' (microtubules) are seen to connect to chromosomes and to the outer cytoplasm.

drawings in his groundbreaking volume, *The Cell in Development and Inheritance*. So here, too, new artistic techniques were used to help forge a new science. And the depictions of mitosis led the way.

And, as has been mentioned in these papers, the epigenetic landscape was first presented as an interaction between biologist Waddington and his good friend, the artist John Piper. In this volume, K. Lee Chichester explicates how Waddington came to see art and biology as syncytial creative processes and believed that Action Painting (in the manner of Jackson Pollock) was a way for scientists to free their imaginations as well as their bodies. Waddington, after all, joined embryology, evolution and genetics into a synthetic field he called 'diachronic biology', a biology of change and process that we would now call 'evolutionary developmental biology' (Waddington 1975; Gilbert 2000). Moreover, he also invented the term 'homeorhesis', whereby cells on this landscape retain their developmental trajectories despite perturbations, keeping their identity while changing their metabolisms. Adult cells may have 'homeostasis', but cells in the processes of developing must express homeorhesis (Matsushita and Kaneko 2020). New ideas in biology need new representations and new images. The field of developmental genetics needed a diagram that would integrate genetics into a developmental framework, indeed a framework wherein the genes helped control developmental processes. The epigenetic landscape was the model that gave the data new meaning (Borish and Gilbert 2016; Nicoglou 2018).

Gardens of forking paths: Isomorphic pathways of cells, proteins and philosophy

In this volume, we find separate papers that have isomorphic properties. The path on which cells acquire their fate, the path on which proteins acquire their form and the path by which investigators find their provisional truths appear to be the same, or at least, homologous pathways.

Let us say at the outset: 'Nothing in cell biology makes sense except in the light of protein folding'. Whether it's enzymes and their substrates, antibodies and their antigens, hormones and their receptors, sperm binding proteins and the egg recognition sites, signalling pathways, DNA synthesis or protein synthesis, it's all about the interlocking shapes formed by protein folding (Gilbert and Greenberg 1984). Protein folding determines binding-specificity and, where needed, catalysis. There is a sculptural dimension to this protein folding. Terrence Deacon, in his analysis of absence (Deacon 2012: 9), points out that 'hemoglobin is exquisitely shaped in the negative image' of the oxygen molecule it will carry, 'like a mold in clay'.

What is striking about Gemma Anderson-Tempini's presentation is the similarity of protein folding to embryogenesis. This was a synthetic idea that goes back to the early era of phage genetics, where the intricate coordination of viral proteins and nucleic acids was (and is still) described as a morphogenetic process (e.g. Israel et al. 1967; Benler et al. 2020). First, Anderson-Tempini has commented on the similarity of the funnel diagrams of protein folding to Waddington's model of the epigenetic landscape, which is not unlike her mazes on a cone. These topologies are used as developmental landscapes. It is also interesting that Waddington's original notion of epigenesis (before he and Piper made it a 'landscape') was one of the sequential cones, where the cell would fall into more stable states until it was finally at rest (Needham 1936).

Second, when Anderson-Tempini, Verd and Jaeger use 'drawing to extend Waddington's epigenetic landscape', they do so by forming models that look remarkably like the protein folding diagrams of Jane Richardson. Their 'Somitogenesis/Oscillations Knot', for instance, looks like an alpha-helix folded in on itself. Remarkably, the Kline bottle model presented in their conclusion is very much like a properly folded protein, with its structure stabilized by the different levels of noise on the inside and outside of the bottle. The Kline bottle model is also an Ouroboros, a figure that Waddington repeatedly doodled and even reprinted in an autobiographical statement (Waddington 1975; Ingram 2019).

Third, the models that are proposed for both the epigenetic landscape and protein folding are models wherein the interacting parts 'seek' their lowest energy levels. The thermodynamic stability of the protein folds is very similar to the 'basins' of gene regulatory networks that represent the resting states of cell differentiation (Huang 2009).

In both of these cases, protein folding and cell fate determination, we see a process very similar to the one that Chiara Ambrosio ascribes to Charles Sanders Peirce. Here, the concept of inquiry is paramount, and drawing can be seen as a method of taking one from a position of irritation and doubt to a healthier position of temporarily settled belief. In other words, one goes from the pluripotent and disturbed condition to a singular secure position. Dr Ambrosio shows that Peirce used diagrams throughout his lectures, and she analyses Pierce's trope of the serpentine line and the brick wall in his 1903 lecture at Harvard. The serpentine line traces the path from perception to an 'abductive inference', a conclusion that was the best plausible explanation available, but which was not proven beyond a reasonable doubt. In his critiques of perception, Peirce loops a serpentine line around itself to make what looks like a brick wall. The line and the wall are both possible, and both are judgements. They are equilibrium positions, not unlike the equilibrium position of a folded protein or a stable cell type.

And the intellectual quest may be another example of such attempts that start with doubt and travel through various pathways before reaching relative certainty and calm. Dr Ambrosio's use of Richardson's diagrams is wonderfully Peircean: What is sometimes difficult to see in the complex foldings of the helices and sheets is that the protein is actually a linear array of amino acids. The protein is Peirce's serpentine line, and it has the ability to fold in several ways. It is the ideal example of a pragmatic drawing epistemology. Morange (2011) has written that Richardson's investment in the ribbon diagrams had three sources: (1) an interest in the evolutionary classification of proteins; (2) the view that data representation was as important as data accumulation and (3) her sense of aesthetics, and her ability to see patterns between highly divergent objects. It should also be noted that Richardson's BA from Swarthmore College is in philosophy, where she was attracted to the pre-Socratics and Spinoza. She spent a year as a graduate student in philosophy before deciding it was not for her (Roseberry 2007).

Moreover, in providing the drawings done along the pathway to her final drawings of folded proteins and epigenetic landscape, Anderson-Tempini is showing the morphogenesis of the model, as it interacts with her own art. The art and the science become mutualistic partners, and the path in the morphogenesis of these models is shown by their succession of embryonic forms. Anderson-Tempini alludes several times to Kaufmann's model of 'The Adjacent Possible'. Only certain things can transform into others, depending on what possibilities are open and which are closed. This idea can be derived from the epigenetic landscape, and Kauffman shows that novelty becomes possible when adjacent modules can interact with one another. And perhaps Anderson-Tempini's bringing together artists and scientists is precisely designed to create new adjacent possibilities. Taking a protein through a maze from native protein to stable protein becomes a social interaction, a 'drawing lab', where people pool their knowledge and their imaginations. The image becomes interactive through the drawing process, and there are many routes to the same end. As Anderson-Tempini notes, the maze becomes a mandala, which, like the sand mandalas of Buddhist artists, are collective creative endeavours that invite meditation and reflection.

Anderson-Tempini's fascinating idea of a fluid maze links protein stability with flux. It would be interesting to use this idea to model the changes in conformational states that a protein assumes when it binds to its partners. Such binding is said to be 'induced fit' rather than 'lock-and-key', indicating that there are stable changes that are made that are critical for protein functions (Koshland 1995). This may also indicate why chaperone proteins are needed to keep the signal transduction proteins in functional states. These chaperone proteins are often thought of as nurses or aid-givers to help proteins fold properly. Seeing them (as Anderson-Tempini and colleagues do) as trained yoga instructors may give us new appreciations of their functions. As Jonathan Philips mentioned in his chapter, even the act of vision demands that the maze shifts as the photons interact with the retinal proteins. And if we are willing to employ the metaphor of 'chaperones' to stabilizing proteins, why not 'yogis'?

Philips also mentioned that the interactive and social modes of drawing provided a new, ‘intuition-first’ rather than ‘maths-first’, entry into the scientific field. Protein folding has a high barrier of initiation caused by physical chemistry and mathematics. The artistic model builds on exploration and randomness. As he said in the discussion, the students ‘are being the protein in a way’. Also importantly, Anderson-Tempini mentioned that each drawing was an experiment. As artists know, each trial of art is an experiment; it involves conceptualization, execution and interpretation. And like most scientific experiments, most paintings, most ceramic bowls and most glass vases get thrown into recycling bins.

A caring for the organism

There are many worlds on this planet. The worlds of the amoeba or sperm are not the world we live in. In addition to each organism having its own perceptual *Umwelt*, different animals and cells actually live in different physical universes. How to render these universes palpable to us *Homo sapiens* is a formidable task for art and science. It takes us from ‘matters of fact’ to ‘matters of concern’, something capable of a science slowed down and made observant through art. Latour (2004: 232) has asked, ‘Can we devise another powerful descriptive tool that deals this time with matters of concern, and whose import then will no longer be to debunk but to protect and care, as Donna Haraway would put it?’ One tool may be an artscience whose goal would not be merely to understand but also ‘to protect and care for matters of concern’ (Stengers 2017).

In such artscience, experimental staging is crucial and would consist of invitations for collaborative organisms. The organisms would therefore be partners who work with the scientists who eventually would speak for them. This is not a futuristic concern. Such collaborations have recently been accomplished in the restoration of the Chesapeake Bay. For over a century, the rallying cry of environmentalists had been to save the oyster from extinction. However, when scientists found that the oyster had the ability to filter the waters of the bay and degrade its pollution, the cry became ‘Save the bay – plant oysters’. The oysters became partners with the conservationists (Gilbert 2019). More recently, oysters are being enrolled as partners to restore the Hudson estuary by forming living breakwaters around Manhattan. The project is only half-jokingly called ‘Oystertecture’ (Wakefield and Braun 2019; Klineberg 2021).

The terms ‘artscience’, ‘oystertecture’ and others are kin to Donna Haraway’s (Haraway 2003) ‘natureculture’, the absence of boundaries between the ‘natural’ and the ‘human’. As Chakrabarty (2009: 201) proclaimed, in the Anthropocene, one sees ‘the collapse of the age-old humanist distinction between natural history and human history'. This collapse means a great deal for art. Heather Barnett spoke on the wondrous abilities of slime moulds to explore space (and time) such that it makes cost-effective decisions on where to proliferate and extend. *Physarum polycephalum*, an acellular slime mould, wherein thousands or millions of nuclei co-exist within a common enormous cytoplasm, was given invitations to explore new environments. Here, these moulds were able to find the shortest path through complex mazes (Nakagaki et al. 2007; Reid and Beekman 2013). They optimized their cell shape, vein network and growth according to external stimuli. Barnett emphasizes the role of *Physarum* as co-creator of their artwork, forming a sympoietic relationship across kingdoms in order to create something novel. Co-creation mandates collaborative and hybrid techniques and methods of playing between the size and time scales at opposite ends of the living spectrum. Barnett's experiments are also artistic inquiries, and this method of revelation employs 'hybrid artistic and scientific methods'. The word 'hybrid' indicates a fusion of art and science into a single agency.[4]

One example of care is to respect the world that cells or organisms live in and to appreciate what entanglements they may struggle with. Part of our anthropocentrism comes from our expectation that the rest of the planet lives at high Reynolds numbers, as we do. Those of us cognizant of living in a high Reynolds number world, where gravity dominates over viscous forces, need to understand that while we may share the same planet, even the same acreage, as slime moulds, insects and microbes, we inhabit different worlds. Even the cells of our body inhabit a different world than our body does, an *Umwelt* of haptic and chemical sensation, where viscous forces play a far greater role than gravity. To create relational encounters between humans and an acellular slime mould, to technologically and artistically mediate interactions between phyla whose sense of time and space may be unrecognizable from ours, is to meet sincerely with an organism as foreign from humanity as one might imagine. The notion of process is underwritten by the temporal dimension, the '/dt' term. So what is the process of an organism who senses time and space differently than we do and how can artistic technology translate the stories of *Physarum* into a human consciousness?

Although *Physarum* is neither an animal, a fungus, nor a plant, there are things we share. The movements of *Physarum*, the contractions and extensions of its cytoplasm, are based on the activation of protein fibres by calcium ions. Indeed, such calcium-activated protein activation is also found in humans. This calcium-mediated changes in cytoskeletal proteins (a wonderful example of protein folding at work) causes the beating of our hearts as well as the movement of the human sperm and the activation of the egg (Panfilov 2017; Barresi and Gilbert 2019). These calcium-induced waves establish the rhythms of mitosis. It would be interesting to back up a moment and look at the calcium-induced waves as creating both the human and the slime mould. Perhaps we can co-create because we have the same equipment in our toolboxes. Barnett has shown that the combination of art and science can help us grok the *Umwelt* that pervades our soils and ocean floors, respecting the world and world-view of our very significant others.

The importance of artscience for care is also demonstrated in James Wakefield's manual for depicting cellular objects. There is no such thing as an uninterpreted cell (Gilbert and Braukman 2011), and 'attending' is critical to a proper interpretation. This attending can include drawing exercises and rituals to focus the attention of the mind as well as the lenses of the microscope. Science is a craft, and the repetition of crafting processes and the feel for the material one works with allow for creativity (Gilbert 2018). Indeed, they help cultivate the heightened corporeal awareness that Deleuze called 'the apprenticeship of the unconscious'. Art can help slow science, make it more responsive and make it more accurate. As Pirsig (1974: 206) had noted, 'Assembly of Japanese bicycle require great peace of mind'.

And sometimes Nature is the consummate artist. As Wahida Khandker has pointed out in this volume, few phenomena show nature's 'artistry' better than mimicry and crypsis (we conflate crypsis, masquerade and transparency as modes of avoiding being seen). As James Wakefield pointed out, mimicry can be physiological or evolutionary. The physiological mode is active, while the evolutionary mode is a passive mode wherein those organisms that look enough like the model organism have a higher probability of not being eaten. While *Physarum* is obviously moving towards a target (i.e. food), those organisms that evolutionarily mimic another organism or attempt to remain hidden in the environment are also 'moving' towards a goal, if only metaphorically. They are climbing up the fitness peaks on the adaptive landscape. While sperm and slime moulds show their goal-directed behaviour by physical movement, those animal lineages evolving towards mimicry or crypsis have a goal that is something else – a poisonous butterfly, a dead leaf or any other item that would allow them not to be seen as prey. The slime mould and sperm (and, for that matter, the cuttlefish) can move to their goals physiologically; the animal lineage heading towards mimicry or crypsis moves evolutionarily.

Nature's art and improvisational skills are seen when changes in the environment cause changes in the camouflage. When eggs of the moth *Nemoria arizonaria* hatch on oak trees in the spring, the caterpillars resemble the seed catkins of the oak trees. However, when they hatch in the summer (when the catkins are gone), they resemble young branches. The leaves (which are full of tannins in the spring) appear to control which shape, colour and texture are produced. Similarly, the butterfly *Bicyclus anynana* has two adult phenotypes. The dry (cool) season morph is a mottled brown butterfly that survives by resembling the dead leaves of the forest floor. The wet (hot) season morph, which routinely flies, has large ventral spots that resemble eyes and which deflect bird and lizard attacks (Brakefield and Frankino 2009; Prudic et al. 2015). The patterns and colours are determined by a heat-sensitive expression of the hormone ecdysone, which, if expressed at high levels, induces the eyespot and other warm-season changes (Brakefield et al. 1996; Oostra et al. 2014).

Artscience allows us to use both biological and artistic knowledge and technologies to allow us to *feel* the integration of organism and environment on a greater-than-intellectual level. It allows us an affective as well as rational means of apprehending the world. Watts (1970) and Sagan (2004) have argued that while biologists and physicists intellectually know that the organism and the environment are not two separate things – but are rather a single process, a unified field – they don't necessarily *feel* that this is so. This is what artscience can do. It can help us slow down, feel and even care. Artscience could create what Stengers calls 'ambulent practitioners', scientists who saunter rather than march, and who would notice, care and let themselves be intrigued (Stengers 2020). Such ambulant, 'earthly' scientists would integrate their knowledge with 'a set of collective non-scientific activities' to do the very practical work of generating a science where matters of earthly concern predominate over those of abstract rationality. Human exceptionalism would have no place in such a view of life, wherein organism and environment are constantly generating each other. The art of the artscience would convey the affective as well as the intellectual modes of the science partner. Indeed, in one of the first uses of the word 'artscience' (Root-Bernstein et al. 2011: 63), it is characterized as 'integrative collaboration to create a sustainable future'.

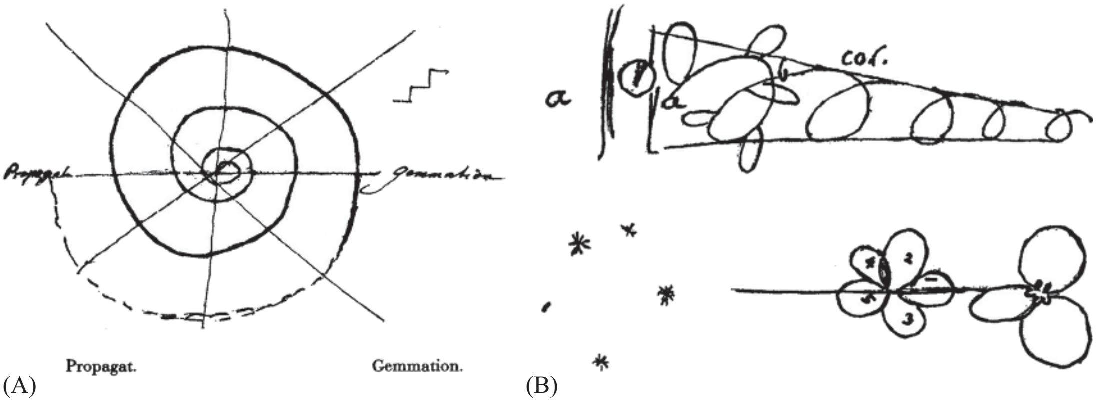
Coda: Goethe's *aperçu*

Such integration of art and science, rationality and imagination brings us to Goethe and Romantic Biology. Janina Wellmann (Wellman 2017) and Gemma Anderson-Tempini (Anderson-Tempini 2019) have written about Goethe's theories of organic motion and his 'gentle empiricism'. James Wakefield also mentioned Johann Wolfgang Goethe, for whom intuition, poetry and music were as important to the scientific enterprise as observations and mathematics (Richards 2002). Goethe's ideas of aesthetics and metamorphosis were critical to the art-science collaboration of Pander and D'Alton, mentioned earlier (Schmitt 2005). Figure A.3A presents Goethe's hand-drawn image of a plant's life spiral. That's not 'life-cycle (*Lebenszyklus' Lebensgeschichte*) but '*Spirale*'. Circles are complete and perfect; life isn't. Mathematically, the circle is merely the bounded collapse of the spiral. It is complete, but life goes on.

In his 1829 *Zeichnung zur Spiraltendenz der Vegetation*, Goethe claimed that plants have a *Spiraltendenz*, a spiral tendency, alternating between asexual budding (gemmation) and sexual seed reproduction (proliferation) as they grow (Goethe 1829). Thus, plants had agency, and they were actively productive. This is beautifully represented by the dotted line of the spiral, which has yet to come. By linking life patterns to activity, Goethe was able to show his dynamic life history for plants and was able to free his explanations from the norm, which had emphasized their teleological aspect and their place in God's creation (Rupik 2021).

Goethe's theory of development demanded that the eyes of the body (taking in the particulars) and the eyes of the mind (knowing the model) had to act together to synthesize how the plant develops (Klausmeyer 2021). Goethe came to this notion of spiral tendency with botanist Karl Friedrich Philipp von Martius in 1828, who noted the spiral paths of leaf formation on new stems. Goethe appeared to be happy to subsume his earlier work into the grander all-encompassing spiral model of plant development. In his late works in plant development, Goethe insists, 'We must assume that a universal spiral tendency presides in vegetation through which, in connection with vertical striving, every structure, every formation of plants, is achieved according to the law of metamorphosis' (Goethe 1828). The result is a plant that has a helical structure (Figure A.3B).

The spiral line is Goethe's 'line of love', the line of affinity and the line of embracement. Goethe called the tendency to form spirals the 'basic law of life' (Müller and Tsuji 2017). Mainberger (2010) has written that 'the spiral' became a kind of intersection point of the author's aesthetic and scientific interests, including the vitality of youth, eroticism, dance, physiognomy and even death. (In July 1831, Frederic Soret wrote that 'He is more than ever obsessed by the spiral tendency'. Goethe



(A) (B)

FIGURE A.3A and B: Goethe's spiral and helix. (A) Spiral of plant life passing through gemmation (asexual reproduction) and prolifikation (sexual seed production) from his *Zeichnung zur Spiraltendenz der Vegetation* (1829). (B) Helical growth of plants from J. W. Goethe and K. F. P. Martius's *Zeichnungen zur Erläuterung der Spiraltendenz der Vegetation* (1828). From Klausmeyer (ref. 55).

died within that year.) This spiral line represents open-endedness and possibilities. It is unbounded, yet it shows prior history and constraints. It is returned with a difference. Interlocking spirals symbolize enmeshment, even life, and it may be an excellent form to represent the integrated life cycles of symbionts.[5] The spiral and helix are primary forms in nature. A human sperm, for instance, swims in a spiral fashion towards the egg. Moreover, in addition to carrying a set of double helices in its haploid nucleus, the midpiece of the tail also contains 'a double-helical structure called the mitochondrial sheath'. This sheath of mitochondria wraps produces the energy for human sperm propulsion (Hirata et al. 2002). In addition, at the tip of the tail, connecting the microtubules to the cell membrane is a helix, 'the tail axoneme intra-luminal spiral' that may help sperm swimming by preventing microtubule disassembly (Zabeo et al. 2018). That's four sets of spirals for the sperm.

Perhaps spirals (and their three-dimensional helices) can be used to represent the interacting lineages that form holobionts, and this representation can be used in attempts to model the five-dimensional organism of evolutionary developmental biology (the three physical dimensions, developmental time and paleontological time). Spirals and helices, derived from Goethe's model and from modern science, can symbolize the rule-bound, incomplete and open-ended growth that is open to experimentation with environmental change. Indeed, new depictions of the evolutionary history of the earth may be expanding from tree models to those of networks and spirals (Ricou and Pollock 2012).

One such model, consciously constructed to represent intersecting life cycles and anti-essentialism is Ursula K. Le Guin's 'Heyiya-if', a set of interlocking spirals (Figure A.4). This symbol is seen in many permutations throughout *Always Coming Home* (Le Guin 1985), where it structures the lives, architecture, music,

FIGURE A.4: A Heyiya-if, a diagram representing interlocking lives from Ursula K. Le Guin's *Always Coming Home*. Original by M. Chodos-Irvine; made available from Creative Commons.

poetry and philosophy of the Kesh people. This interlocking spiral motif is also seen in art, at least as ancient as the tomb of Egyptian queen Nefertari (died *c.*1255 BCE), on whose tiles this design is wrought. It can be formed by cupping one's fingers into the palm of the opposite hand. Such an accessible form might be a fitting diagram for what it means to be holobiont.

Biology and its representations have a positive feedback on each other. As changes in science demand changes in its representations, the newly formed representations will promote and stabilize only those particular perspectives of the science. They would enable new questions to be asked and would also channel the mind into these new directions. Representations are both creative and constrictive. Therefore, one representation should not be thoroughly hegemonic. Indeed, Stengers (2018) contends that if science could free itself from its current mercantile model, it would develop into multiple modes of science. Such a pluralistic biology would have multiple modes of representation. Recognizing the mutualistic symbioses between biology and art may help bring about such new ways to depict biology as a process. This book is an embryonic landmark on the way to such representations.

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NOTES

1. It is now known as the Harvard Museum of Comparative Zoology. Agassiz's name is being dissociated from many monuments due to his attempts to justify racism through science. Some of these attempts used art, specifically photographs of naked Brazilian slaves. In a recent symposium concerning, these photographs, de la Fuente (2021) noted, 'Artists are protagonists in this process of knowledge production'.
2. Drawing, painting, music and dancing are neither luxury items nor educational peripherals. Rather, empirical evidence shows them to be critical, perhaps mandatory, parts of scientific education. As Michèle and Robert Root-Bernstein (1989, 2013) have shown, art background and success in science have an almost linear relationship. 'The more arts and crafts that scientists, engineers, and entrepreneurs engage in across their lifetimes, the greater the likelihood of achieving important results in the workplace' (Root-Bernstein and Root-Bernstein 2013). Indeed, the best predictors of whether a college student will succeed in mathematics and science are their scores on visual imaging and visual memory tests (Winner and Casey 1992). On these tests, students who excel in the sciences outperform art majors.
3. Sonrel became a major photographer in the remarkable city that was Boston in the 1860s and 1870s, making *carte de visit* portraits for the likes of Oliver Wendel Holmes (both

senior and junior), sculptor Anne Whitney, mathematician Benjamin Peirce (Charles Peirce's father), and Louis Agassiz and his wife.

4. Biologically, 'hybrid' indicates a complete fusion between two entities, whereas 'chimeric' indicates that the two entities have come together but retain their separate characters. Classes that are simultaneously live and online are really 'chimeric', not 'hybrid'. One of the authors (S. R. Gilbert) of this book has co-constructed art with bark beetles, whose curvilinear tubes in tree branches were used to inform musical notes on a player piano. New installation-like mesocosms are now being created as a middle ground between the uncontrolled natural environment and the regimented conditions of the laboratory. This allows substantial cooperation with the more-than-human.
5. The spiral of life metaphor is also used in Suzanne Simard's *Finding the Mother Tree* (Simard 2021), which is largely about the critical importance of symbiosis for the plant survival.

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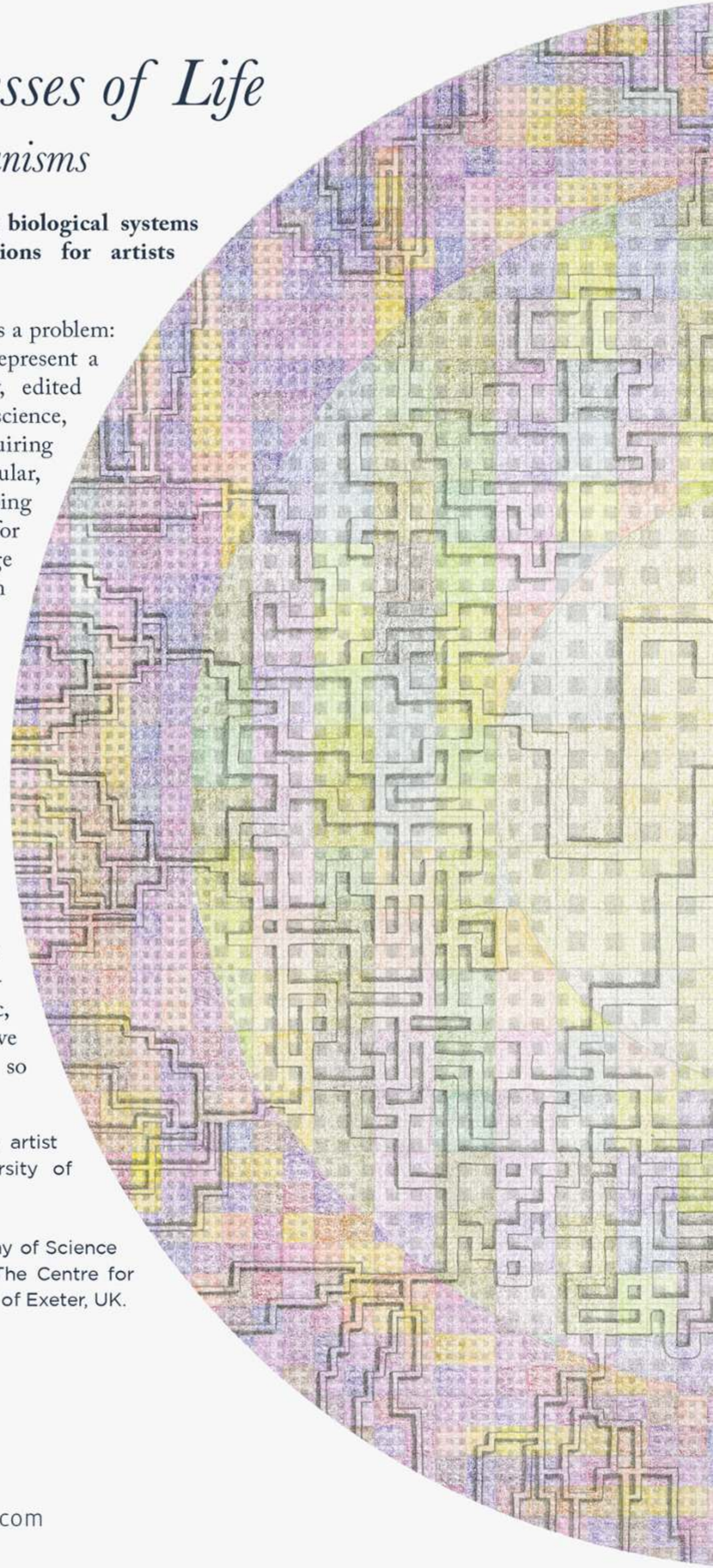
Drawing Processes of Life

Molecules, Cells, Organisms

How the challenge of depicting biological systems can generate productive questions for artists and scientists.

An artist drawing cell division faces a problem: what is the best way to visually represent a dynamic process? This anthology, edited by an artist and a philosopher of science, explores drawing as a way of inquiring into living processes at the molecular, cellular, and organismal scale. In doing so, drawing emerges as a tool for relaying and uncovering knowledge – a pathway for research, not an end result.

Incorporating drawing studies and contributions from scholars in the humanities and life sciences, *Drawing Processes of Life* addresses epistemological issues arising in cell division, insect metamorphosis, protein folding, and other ever-shifting biological systems. Fulfilling the promise of an interdisciplinary collaboration between artists and scientists, this book demonstrates the interweaving of processes, scientific, artistic, and non-human that the abstractive techniques of modern science so readily obscure.



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