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Compelled by the Diagram

Thinking through C. H. Waddington's Epigenetic Landscape

Matthew Allen

Abstract

Between 1940 and about 1960, Conrad Hal Waddington produced several illustrations to explain a concept central to his theories of developmental biology. The concept Waddington explained, the epigenetic landscape, was not based on settled science, and its implications were not easy to grasp. Unlike proponents of the most successful contemporary biological theory, Waddington was committed to including all biological phenomena—no matter how complex or unusual—in a single theoretical system. His intellectual style and use of images matched his ambition. Waddington used compelling images to get his readers to engage with and work through his theories. His images used a shifting, even contradictory, set of metaphors and analogical models, from train yards to crafted topological surfaces. Through an analysis of Waddington's images and theories, I show that taking a close look at what scientific images show and how they show it is important for the historiography of science. Images can be effective at drawing viewers in, confounding them, and prodding them to ask questions; this is one reason images are necessary for science.

About the Author

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Compelled by the Diagram

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The images used by Conrad Hal Waddington (1905-1975) to explain what he called the epigenetic landscape have received significant scrutiny in the past decades, both inside the field of biology and out.¹ Their allure is understandable. Though these illustrations depict simple, realistic things (such as balls about to roll down surfaces), they are central to the almost miraculous cognitive process through which a viewer comes to understand a complicated set of concepts. The last of Waddington's illustrations of the epigenetic

landscape (Fig. 1) shows a ball poised at the top of an undulating surface. The paths the ball may take represent the branching process of cellular differentiation that occurs during embryonic development. Beyond this type of theoretical content (which I will unpack below), Waddington's images carry connotations of the intellectual context in which they were produced. They suggest, for example, that someone—the experimental biologist—has hands-on control of the developmental process. Thus Waddington's illustrations are alluring because they serve as a focal point, both for biologists hoping to understand development and for historians who want to understand Waddington's intellectual project. In scientific practice, allure is sometimes necessary.² Waddington's images were a crucial part of his intellectual project, which I will show through an analysis of what they represent and how this relates to Waddington's style of reasoning.³

Though it perhaps became increasingly unusual through the course of the past century, Waddington's style of reasoning belongs to a recognizable type. Waddington has been described as a "true twentieth-century polymath"; one reviewer notes that "no modern funding agency would allow any individual to undergo so many changes of interest and direction."⁴ Waddington began his career in the 1930s as an experimental biologist, publishing articles in specialist journals such as *Nature* and the *Journal of Experimental Biology*. In the 1950s and 1960s, Waddington wrote ever more frequently about ethics and the role of science in society, and, like many scientists, towards the end of his career he

¹ For their reception in biology, see, e.g., Scott F. Gilbert, "Epigenetic Landscaping: Waddington's Use of Cell Fate Bifurcation Diagrams," *Biology and Philosophy* 6 (1991): 135-154; and Melinda Bonnie Fagan, "Waddington Redux: Models and Explanation in Stem Cell and Systems Biology," *Biological Philosophy* 27 (2012): 179-213. Waddington's diagrams also had an influence in, for example, architecture in the early 1990s; see Sanford Kwinter, "Soft Systems," in *Culture Lab 1*, ed. Brian Boigon (Princeton, NJ: Princeton Architectural Press, 1996), 207-228. This paper focuses on biology; the influence of Waddington's images, intellectual project, and style of reasoning on thinkers in other disciplines will be a topic for future research.

² For a discussion of the necessity (or not) of images in science, see, e.g., Michael Ruse, "Are Pictures Really Necessary? The Case of Sewell Wright's 'Adaptive Landscapes,'" in *Symposia and Invited Papers*, vol. 2 of *PSA: Proceedings of the Biennial Meeting of the Philosophy of Science Association* (1990), 63-77; James R. Griesemer, "Must Scientific Diagrams Be Eliminated? The Case of Path Analysis," *Biology and Philosophy* 6 (1991): 155-180; and Laura Perini, "Diagrams in Biology," *The Knowledge Engineering Review*, 28, no. 3 (2013): 273-286.

³ I am sympathetic to Ian Hacking's "styles project." Ian Hacking, "'Language, Truth and Reason' 30 years later," *Studies in History and Philosophy of Science* 43 (2012): 599-609.

⁴ Jonathan M. W. Slack, "Conrad Hal Waddington: the last Renaissance biologist?," *Nature Reviews Genetics* 3 (November 2002): 889-895.

tackled broad questions ranging from philosophy to art.⁵ Early on he picked up a dialectical style of thinking from the philosopher Alfred North Whitehead, which manifested itself in his conversational style of prose. Waddington is often described as “ahead of his time”—he is best known as a grandfather figure for the evo-devo movement, which remains controversial.⁶ Because his work was against the grain, and thus in constant danger of being dismissed, Waddington employed images to draw viewers in and get them to unpack and think through his theories. He used images to keep possibilities open in a situation in which his audience might otherwise settle on simple—and, in Waddington’s view, *false*—certainties.

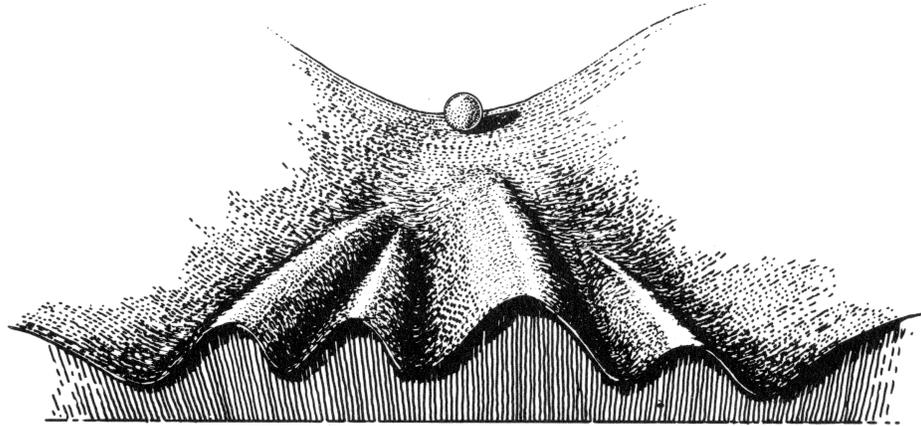


Figure 1

The Epigenetic Landscape, from Conrad Hal Waddington, *Principles of Development and Differentiation* (New York: Macmillan, 1966), 49 (photo: author).

Two Styles

Biology in the 1930s, the period of Waddington’s intellectual formation, was dominated by the modern evolutionary synthesis.⁷ The neo-Darwinian evolutionary theory that was an outcome of the synthesis has proved extremely successful—so successful that popular understanding has dropped the “neo-” and equated the modern synthesis biologists’ theory with Darwinism itself.⁸ The modern synthesis embodied a distinctive style. Richard Lewontin, a prominent twentieth-century biologist, offers this description: “The modern skeletal

⁵ For Waddington’s bibliography, see Alan Robertson, “Conrad Hal Waddington. 8 November 1905 – 26 September 1975,” *Biographical Memoirs of Fellows of the Royal Society* 23 (November 1977): 575-622.

⁶ “Evo-devo” refers to a combination of evolutionary biology and developmental biology; see, e.g., Corey S. Goodman and Bridget C. Coughlin, ed., “Special feature: The evolution of evo-devo biology,” *Proceedings of the National Academy of Sciences* 97, no. 9 (2000): 4424-4425.

⁷ It is also referred to as the “modern synthesis,” the “evolutionary synthesis,” the “neo-Darwinian synthesis,” etc.

⁸ See, e.g., Vassiliki Betty Smocovitis, *Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology* (Princeton, NJ: Princeton University Press, 1996).

formulation of evolution by natural selection consists of [several] principles that provide a purely mechanical basis for evolutionary change, stripped of its metaphorical elements."⁹ The theory was bare-bones for a reason. By paring it down to essentials, proponents of the modern synthesis minimized conflicts between its major elements, Mendelian genetics and Darwinian evolution. Theorists of the modern synthesis used a strategy of compromise and diplomacy to create an atmosphere in which to hash out theoretical details.¹⁰

The trouble with the modern synthesis was that "an immense amount of biology was missing."¹¹ Most notably missing was Waddington's own field, developmental biology. The history of how and why the modern synthesis excluded developmental biology is now a matter of disciplinary myth. It was thought that macroevolution could explain microevolution and that there would be no need for morphology or developmental biology to bridge between the two.¹² One consequence was that the finer points of how genetics and evolution fit together were never really worked out.¹³

Waddington's speculation often concerned these very details. The choice between leaving theoretical minutia for later or trying to work through them with the limited means available is a matter of style; both are legitimate ways of doing biology. But style affects substance in subtle ways. An exchange between Waddington and Ernst Mayr, a leading figure of the modern synthesis, highlights the contentions stylistic differences can cause. In 1961, Mayr wrote a widely read essay that divided the biological sciences into distinct domains by mapping approaches to biology onto types of causality.¹⁴ He argued that there are two legitimate types of causal explanation and two ways of doing biology: evolutionary biologists argue from proximate causes while functional biologists argue from ultimate causes. Though they appear to be talking about the same things, evolutionary biologists and functional biologists are in fact using the same words to talk about entirely different phenomenon – "talking past one another," in Mayr's words. The differences between biologists' forms of explanation stem, according to Mayr, from fundamental differences in values and questions:

The functional biologist is vitally concerned with the operation and interaction of structural elements, from molecules up to organs and whole individuals. His ever-repeated question is 'How?'... The evolutionary biologist differs in his method and in the problems in which he is interested. His basic question is 'Why?'¹⁵

Mayr goes on to explicitly reject one last type of causal explanation: final causality, or the idea that nature is somehow planned or designed. Mayr makes a "clear-cut separation"

⁹ Richard C. Lewontin, "Not So Natural Selection," *London Review of Books*, May 27, 2010, accessed June 25, 2015, <http://www.nybooks.com/articles/archives/2010/may/27/not-so-natural-selection/>

¹⁰ This included agreeing on terminology and "changing attitudes;" see Ernst Mayr, "Prologue: Some Thoughts on the History of the Evolutionary Synthesis," in *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, ed. Ernst Mayr and William B. Provine, (Cambridge, MA: Harvard University Press, 1980), 1-48.

¹¹ Lewontin, "Not So Natural Selection."

¹² M. B. Adams, "Through the looking glass: The evolution of Soviet Darwinism," in *New Perspectives in Evolution*, ed. L. Warren and H. Kopyowski (New York: Liss/Wiley, 1991), 37-63.

¹³ Scott F. Gilbert, "Diachronic Biology Meets Evo-Devo: C. H. Waddington's Approach to Evolutionary Developmental Biology," *American Zoology* 40 (2000): 729-737.

¹⁴ Ernst Mayr, "Cause and Effect in Biology," *Science*, 134, no. 3489 (November 10, 1961): 1501-1506.

¹⁵ *Ibid.*, 1502.

between individuals, who can exhibit goal-directed behavior because they have been “programmed” by their DNA to do so, and “the overall harmony of the organic world” (the domain of evolution), which cannot.¹⁶ Mayr raises very reasonable points—his prose reads as a model of reasonableness. Mayr proposes the type of simple, clear-cut distinctions that allowed the modern synthesis to create a working consensus and eventually to triumph over competing theories of evolution.¹⁷

It is no surprise that Waddington wrote a response to Mayr’s essay in the following issue of *Nature*: by 1961 Waddington had been in the habit of writing opinionated letters to the journal for more than two decades, and Mayr’s distinctions cut to the heart of Waddington’s theories. But Waddington’s engagement went beyond the usual letter. Waddington also circulated Mayr’s essay before a conference he organized in 1966 – and he later published it in the conference proceedings bookended by two critical essays of his own. Here is part of his response, on the topics of final causes:

It is becoming inadequate to point out, as Mayr does, that natural selection is not purposive. In itself it is of course no more purposive than is the process of formation of interatomic chemical bonds. But just as the latter process is the basic mechanism underlying the protein syntheses which are integrated into the quasi-finalistic mechanism of embryonic development, so natural selection is the basic mechanism of another type of quasi-finalistic mechanism, that of evolution. The need at present time is to use our newly won insights into the nature of quasi-finalistic mechanisms to deepen our understanding of evolutionary processes.¹⁸

Waddington demands that “chemical bonds,” “embryonic development,” and “natural selection” be taken into account, all at the same time. For Waddington, there is no way to separate functional biology from evolutionary biology, and he adds to these a third approach to biology that Mayr ignored entirely: developmental biology. While Mayr argues for theoretical synthesis by way of diplomatic compromise, Waddington asks for speculation unencumbered by practical divisions. Mayr later mentioned that embryologists failed to create a “viable bridge” between disciplines, implying that if a concept from developmental biology was not useful for evolutionists, then its exclusion from the synthesis was justified.¹⁹ This is the context in which Waddington argued for what he calls “theoretical biology.” He objects to Mayr’s “cleavage between types of phenomenon,” and he suggests that the “newly won insights” of developmental biology may offer a way to bring all of biology back together.²⁰

The Epigenetic Landscape

To say that Waddington and Mayr employed different styles is to say more than that their prose is different. Waddington and Mayr also had different ways of constructing and

¹⁶ *Ibid.*, 1504.

¹⁷ Darwinism was one among several competing theories of evolution circa 1930; Mayr, “Prologue,” 4.

¹⁸ Conrad Hal Waddington, “The Basic Ideas of Biology,” in *Towards a Theoretical Biology: Vol. 1: Prolegomena*, ed. Conrad Hal Waddington (Chicago: Aldine, 1968), 7.

¹⁹ Mayr, “Prologue,” 40-42.

²⁰ Waddington, “The Basic Ideas of Biology,” 7.

testing theories, which lead to different ways of using images.²¹ If a skeletal theory like the modern synthesis is developed through logical propositions, more fleshed-out theoretical styles often employ analogical models. The place of models and metaphors in scientific inquiry was a subject of heated debate in the 1950s and 1960s.²² Critics of logical positivism noticed the slippery relation between features of models and theoretical propositions.²³ Thinking of an atom as being something like a solar system, for example, helps explain some theoretical observations (which is why Ernest Rutherford and Niels Bohr proposed the model in the first place), but it also raises questions. The planetary model may help describe hydrogen atoms, but what about atoms with more than one electron? Testing questions raised by models is often productive, sometimes by leading to a new model and different questions (as happened with the Bohr-Sommerfeld model and eventually the Schrodinger model of the atom). Models, metaphors, and thought experiments pervade science, but some scientists engage with them more than others. Waddington was a serial modeler, a strategy which supported his approach to theory.

The concept Waddington is best known for, the epigenetic landscape, was developed through analogical models over the course of four decades. Waddington first used the term, which he coined, in 1940. It drew on familiar associations. Epigenesis was a common concept from eighteenth-century biology, and biologists in the mid-twentieth-century would also have known of Sewall Wright's adaptive landscape, which explained adaptation as a genetic drift up and down humps and pits on a topological surface (Fig. 2).²⁴ Waddington's major theoretical contribution was to insist that a complex "landscape" acts as the mediator between genes and an adult organism, emphasizing that all of the "environmental" (or "epigenetic") influences that occur during development cannot be ignored (as they would be by a geneticist thinking in terms of population, as the modern synthesis biologists were).

Waddington used a handful of illustrations to help explain his concept, drawing on metaphors of train tracks, streams of water, and, of course, landscapes. His images and metaphors changed as his theories evolved, and they contradict one another in various ways. It is not always clear whether or not a feature of one of his illustrations refers to something important about his concept; the author of Waddington's retrospective in *Nature* notes that "scientists are still confused by this today."²⁵ As I explain below, this tension between concept and representation does important cognitive work for Waddington.

²¹ The different ways images are used by biologists is a matter of emphasis rather than clear-cut distinction. Though an analysis of, e.g., Mayr's use of images is beyond the scope of this study, a quick look at his publications suggests that he uses illustrations of analogical models less frequently than Waddington. While Waddington typically includes a wide variety of analogical imagery, Mayr's canonical 1942 text, *Systematics and the Origin of Species*, for example, has only one that clearly falls into this category: a rather straightforward depiction of a phylogenetic tree.

²² Roman Frigg and Stephan Hartmann, "Models in Science," *The Stanford Encyclopedia of Philosophy* (Fall 2012 Edition), ed. Edward N. Zalta, accessed June 25, 2015, <http://plato.stanford.edu/archives/fall2012/entries/models-science/>.

²³ For a critical introduction to the contradictions of logical positivism, see Frederick Suppe, "The Search for Philosophic Understanding of Scientific Theories," in *The Structure of Scientific Theories* 2nd ed., ed. Frederick Suppe (Urbana: University of Illinois Press, 1977), 1-241.

²⁴ Anya Plutynski, "The rise and fall of the adaptive landscape?," *Biology and Philosophy* 23 (2008): 605-623.

²⁵ Slack, "Conrad Hal Waddington," 892.

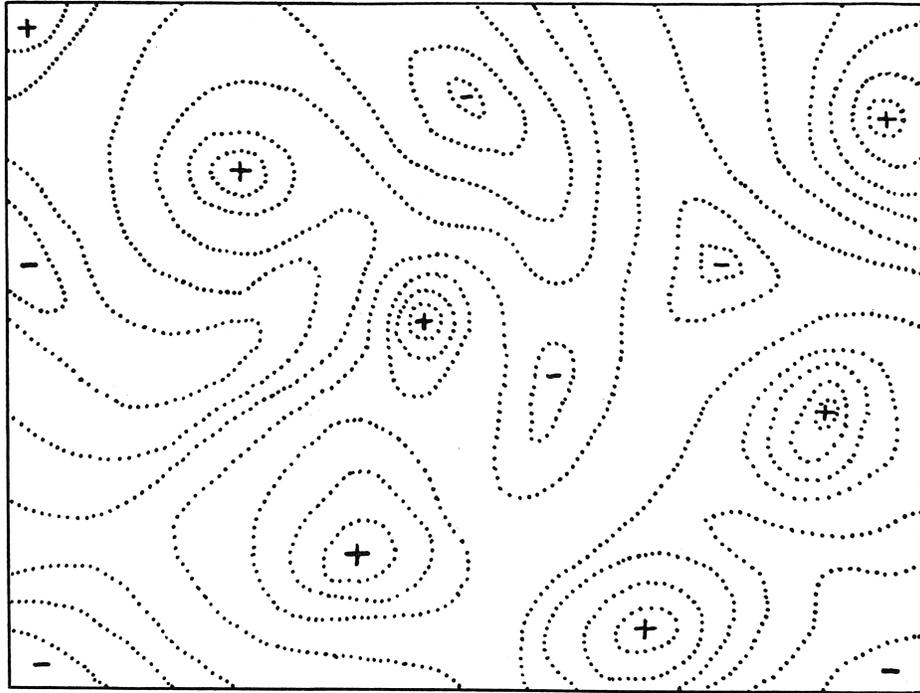


Figure 2

The Adaptive Landscape, from Sewall Wright, "Evolution in Mendelian populations," *Genetics* 16 (1931), 358 (photo: author).

In research leading up to the epigenetic landscape, Waddington sought to work out the mechanisms by which an animal develops from a single cell into an organism with groups of specialized cells. First the single cell divides, and then the resulting two divide, then the resulting four, and so on. At certain points, cells begin to specialize: one region in the developing embryo becomes brain cells, another becomes liver cells, etc. Waddington began illustrating this process with cell-fate bifurcation diagrams (Fig. 3).²⁶ His explanation is that cellular specialization occurs as a "series of branching decisions, taken under the control of genes."²⁷ This explanation was based on his experiments with fruit flies—experiments in which a mutant gene would, for example, make a leg develop on a fly's head in place of an antenna (Fig. 4).²⁸ Waddington suggests that the mutant gene flips a switch, causing a different developmental pathway to be followed.

Grizzly as these experiments were, Waddington's diagram of the process is relatively straightforward. That is, its semantic content is limited; Waddington could easily have described all the paths and switches in words. But his images also carry unstated connotations that nudge the viewer down particular interpretive paths and incidental features that suggest areas for further investigation. The importance of representational choices becomes evident when the different images Waddington used to describe the same concept are compared. One other illustration Waddington used in this early period was a photograph

²⁶ Gilbert, "Epigenetic Landscaping."

²⁷ Conrad Hal Waddington, *Organizers and Genes* (Cambridge, UK: Cambridge University Press, 1940), 12.

²⁸ *Ibid.*, 83.

of a train yard (Fig. 5). The most important theoretical point that comes along with this new metaphor is not apparent in the image, but it comes out in the text: the switching and branching takes place as the train cars move down a hill. As Waddington says:

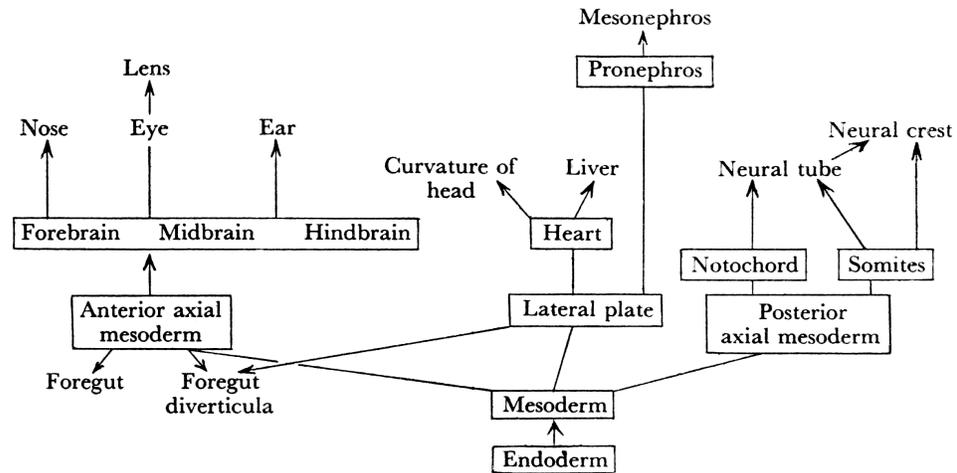


Figure 3

Organisers in the Chick, from Conrad H. Waddington, *Organizers and Genes* (Cambridge, UK: Cambridge University Press, 1940), 12 (photo: author).

You are looking at an incline called the Hump. The wagons are pushed over the Hump and go running downhill and are sorted out by the systems of points into the various sidings. Now an embryo is in some ways analogous to a set of trucks sliding down the Hump.²⁹

This is Waddington's first use of the landscape metaphor (a hump, after all, is a landscape feature), and it raises some new questions. What is the biological equivalent of gravity? What are biological switches made of, and who is switching them? In the era before the discovery of DNA, how exactly something could be "under the control of genes" was a matter of speculation.³⁰

A satisfying description of developmental pathways (which Waddington represented as lines in a drawing or tracks in a photograph) turned out to be illusive at mid-century. Techniques did not exist to conduct the required experiments.³¹ But Waddington suggested some possibilities. To describe where and how shifts in developmental pathways occur, he presents another diagram (Fig. 6), noting that "one can interpret [the action of the mutant

²⁹ Conrad Hal Waddington, *How Animals Develop* (London: Allen and Unwin, 1935), 96.

³⁰ On the history of the gene concept, see Evelyn Fox Keller, *The Century of the Gene* (Cambridge, MA: Harvard University Press, 2000).

³¹ Slack, "Conrad Hal Waddington," 891. One famous failure in which Waddington took part was the "gold rush" to find the "miraculous substance" called the organizer; see J. A. Witkowski, "Optimistic Analysis: Chemical Embryology in Cambridge 1920-42," *Medical History* 31 (1987): 247-268.

gene] in two ways; either it affects both the [secondary] tracks, or it acts much earlier and shifts the whole track system including the branch point."³² In this diagram, the dotted lines represent one of Waddington's interpretations of how the track system is affected by a mutant gene; the thin solid lines represent the other. The visual possibilities of the diagram itself, either shifting the branches or just their endpoints, seem to have suggested to Waddington how the biology might work. The train tracks and the black lines participated in the conceptual development. This is an example of the productivity of images of analogical models.

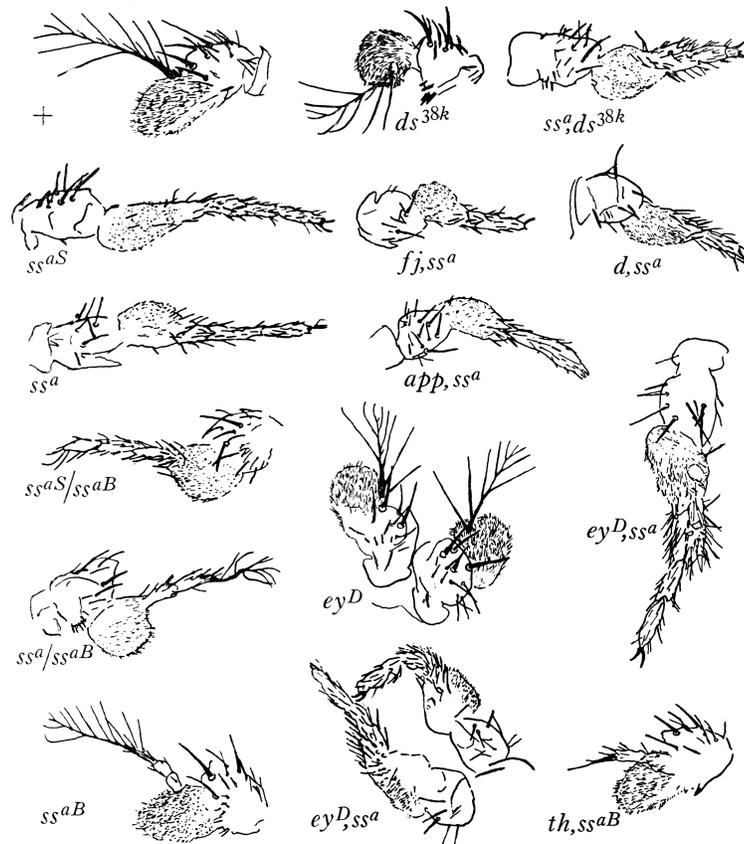


Figure 4

Antennae of the different allelomorphs of aristopedia and of some compounds, from Conrad H. Waddington, *Organizers and Genes* (Cambridge, UK: Cambridge University Press, 1940), 80 (photo: author).

³² Waddington, *Organizers and Genes*, 82.

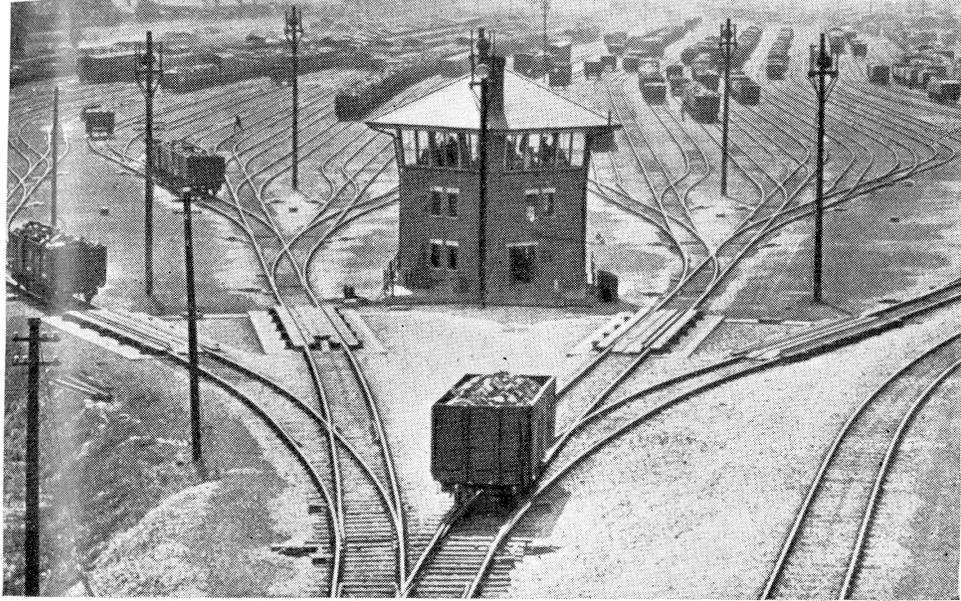


Figure 5

Whitemoor Marshalling Yard, L.N.E.R., from Conrad H. Waddington, *How Animals Develop* (London: Allen and Unwin, 1935), 97 (photo: author).

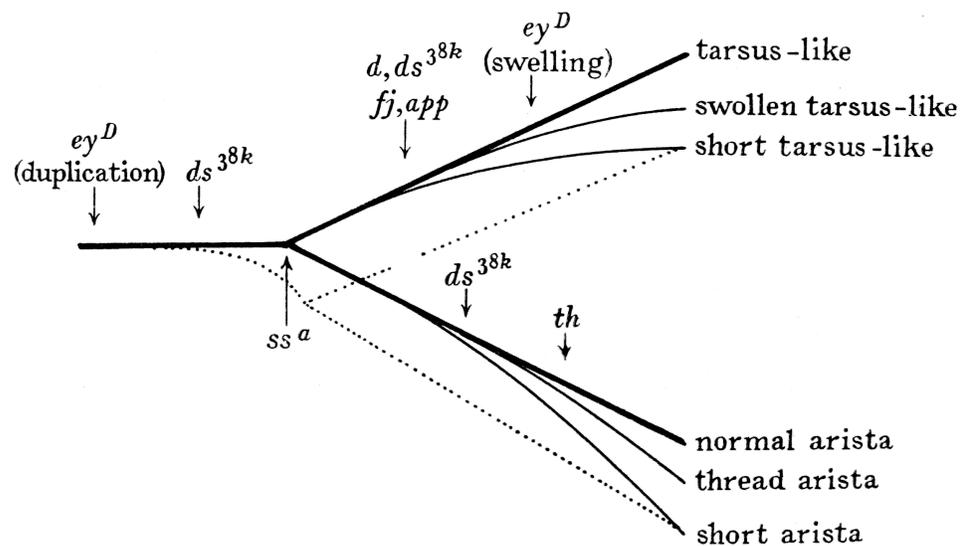


Figure 6

The Aristopedia Developmental Track System, from Conrad H. Waddington, *Organizers and Genes* (Cambridge, UK: Cambridge University Press, 1940), 83 (photo: author).

These illustrations were the precursors to the epigenetic landscape. Waddington's first description of this new concept came in 1939, without his neologism attached. It occurs in the middle of a long discussion of the branching pathways of cellular differentiation:

[W]e have to remember that each branch curve is affected not only by the gene whose branch it is but by the whole genotype. We can include this point if we symbolize the developmental reactions not by branching lines on a plane but by branching valleys on a surface. The line followed by the process... is now the bottom of a valley, and we can think of the sides of the valley as symbolizing all the other genes which co-operate to fix the course of the time-effect curve.... One might roughly say that all these genes correspond to the geological structure which moulds the form of the valley. Genes... which have their main effect at certain branching points are like intrusive masses which can divert the course of the developmental process down a side valley.³³

Waddington introduces the metaphor of a geological surface because the metaphor of branches and switches does not convey the fact that some genes have an effect beyond particular switch-points – they “mould” the landscape more broadly.

Waddington's first illustration of the epigenetic landscape, and his first use of the term, was on the first page of *Organizers and Genes* (Fig. 7). Here Waddington refines the landscape metaphor by illustrating development as a branching system of streams. The flow of water and the gradual erosion of earth replace the mechanical movement of switches, tracks, and trains. But the illustration is not perfect. In his text, Waddington mixes his metaphors:

[T]he system of developmental paths has been symbolized in two dimensions as a set of branching lines. Perhaps a fuller picture would be given by a system of valleys diverging down an inclined plane.... [Development] only takes place during a certain period of time. During this period, the developmental track can be represented as a valley with gently sloping sides; if the course of development is disturbed, the point representing its disturbed state will be somewhere off the track, and if it is still within the valley, the process will regulate by running down the side of the valley until it reaches the normal track at the valley bottom.³⁴

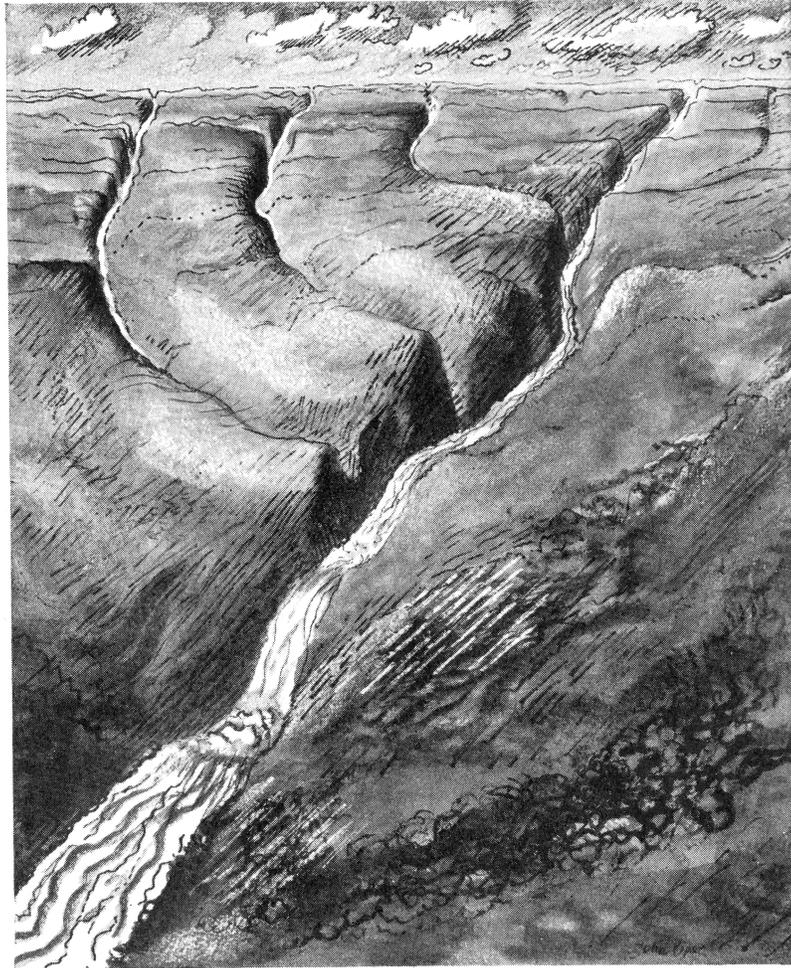
Waddington's description fits neither water nor trains: the developmental process is something that can go off its track, up the side of a valley, and return neatly to the track. This misalignment of metaphors is a signal that something complex and difficult to explain is at work. Waddington's research at the time suggested that developmental pathways are somewhat flexible. Waddington called this phenomenon “buffering” or “canalization,” a concept which has proven to be one of Waddington's most important theoretical contributions.³⁵ The metaphor of a valley conveys part of the idea: if development is pushed off its normal path and up the valley wall, gravity will bring it back. But the valley metaphor is imperfect: it does not make sense to think of water leaving the streambed. The metaphor of a branching system of streams does, however, capture the fact that cellular bifurcation happens along all paths at once. There is no single path in development; cellular specialization proceeds towards many specialized cell-types at the same time. And, generally

³³ Conrad Hal Waddington, *An Introduction to Modern Genetics* (London: Allen and Unwin, 1939), 182-183.

³⁴ Waddington, *Organizers and Genes*, 92-93.

³⁵ Willem Scharloo, “Canalization: Genetic and Developmental Aspects,” *Annual Review of Ecology and Systematics* 22 (November 1991): 65-93.

speaking, this new metaphor suggests a natural process: while trains and tracks are controlled by an outside force, a valley is created by the flow of water itself, just as evolution happens through the process of natural selection without outside intervention.



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 7

The Epigenetic Landscape, from Conrad H. Waddington, *Organizers and Genes* (Cambridge, UK: Cambridge University Press, 1940), frontispiece (photo: author).

There are a few ways Waddington's 1940 illustration of the epigenetic landscape could be elaborated or changed. One would be to show the stream swelling as it proceeds through the valley (embryos grow, after all). Waddington chose to focus attention elsewhere: on the mechanics of buffering. To do this he switched to yet another metaphor. Waddington's next illustration of the epigenetic landscape, from 1956, represents the developmental process as the path followed by rolling eggs (Fig. 8).³⁶ Unlike a stream of water, which can split and recombine, and soil, which would require a feat of engineering to control, this new image suggests well-defined paths and hands-on control. It implies that someone will release the eggs at the top and watch them roll down. The surface looks like a crafted artifact that could be altered to create different developmental pathways. The suggestion of hands-on control hints at the life of an experimental biologist at mid-century, tweaking the developmental environment and running trials on millions of fruit flies.

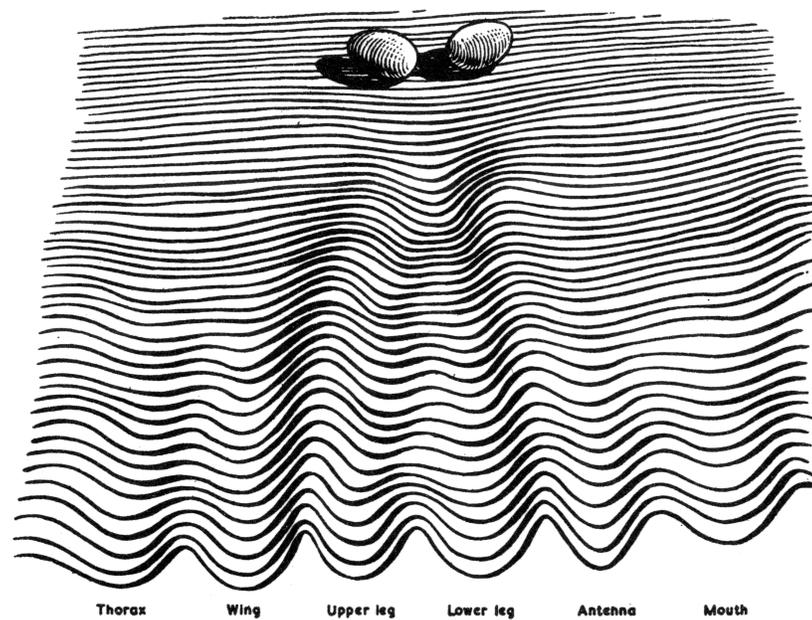


Figure 8

The 'Epigenetic Landscape,' from Conrad H. Waddington, *Principles of Embryology* (London: Allen and Unwin, 1956), 351 (photo: author).

Waddington produced several versions of this illustration. The most refined, published in 1957 in Waddington's best-known book, *The Strategy of the Genes*, shows a single ball and a single set of branching paths as well as the system of "guy ropes" attached to "pegs" that shape the surface from below (Fig. 9). While the first illustration of the epigenetic

³⁶ Conrad Hal Waddington, *Principles of Embryology* (London: Allen and Unwin, 1956), 351.

landscape varied line-type and tone to create a naturalistic image, the ones that followed look like highly stylized engravings of artificial surfaces. These latter illustrations employ a linear technique popularized in the nineteenth-century with fine art reproductions (Fig. 10).³⁷ This style of engraving was developed so publishers could ensure consistency across illustrations even if more than one engraver was employed. Every line looks the way it does for a reason; no artistic license is involved. By using illustrations following this technique, Waddington implies that his epigenetic landscape is as logical and under control as the lines cut into steel plates by a team of engravers. If the earlier drawing of a system of streams fits the big-picture holism of nineteenth-century evolutionary biology, the engraved version fits the hard-nosed experimentalism of mid twentieth-century developmental biology.³⁸ Because Waddington's work was aimed at both camps, it is no surprise that he used illustrations with both connotations. But the fact that he settled on illustrations suggesting precise experimental control reveals his deepest disciplinary affiliation.

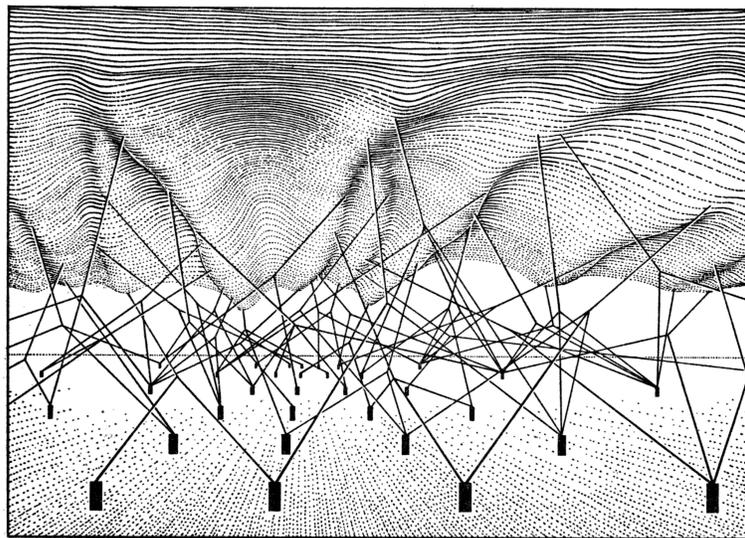
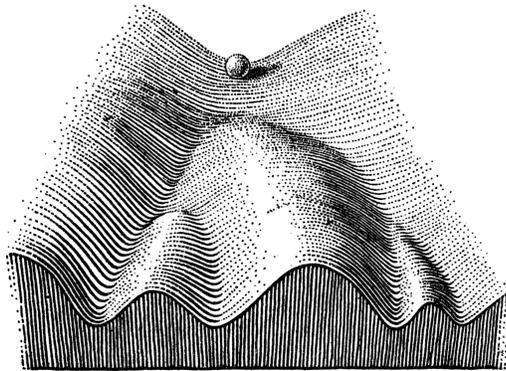


Figure 9

*Part of an Epigenetic Landscape and The Complex System of Interactions Underlying the Epigenetic Landscape, from Conrad H. Waddington, *The Strategy of the Genes* (London: Allen and Unwin, 1957), 29 and 36 (photo: author).*

³⁷ William Ivins, *How Prints Look: Photographs with a Commentary* (New York: Metropolitan Museum of Art, 1943), 76.

³⁸ The rift between experimentalists and those who "worked with whole organisms" began in the middle of the nineteenth-century and grew in the early twentieth; see Mayr, "Prologue," 6.

Waddington used his illustrations to raise questions and to convince others that these questions would be productive avenues of research. For a question to be productive to an experimentalist, it must be precise enough to be tested. Waddington used topographical diagrams with connotations of precision and control to make his most controversial theoretical points. Figure 11, for example, shows a black line that remains in a fixed position in space while the landscape around it is shifted. Waddington used this to help explain an unusual phenomenon, genetic assimilation. This is now an accepted concept:

Faced with changes in their environment, organisms have the capacity to physiologically adapt to these variations by modifying the epigenetic landscape. Genetic assimilation is the subsequent stabilization by genetic variations of this initial physiological adaptation.³⁹



Figure 10

Robert Nanteuil, Enlarged detail from *Engraved Portrait of Jean Loret*, from William Ivins, *How Prints Look: Photographs with a Commentary* (New York: Metropolitan Museum of Art, 1943), 75 (photo: author).

³⁹ Michel Morange, "What History Tells Us: XVII: Conrad Waddington and *The Nature of Life*," *Journal of Bioscience*, 34 (June 2009): 196.

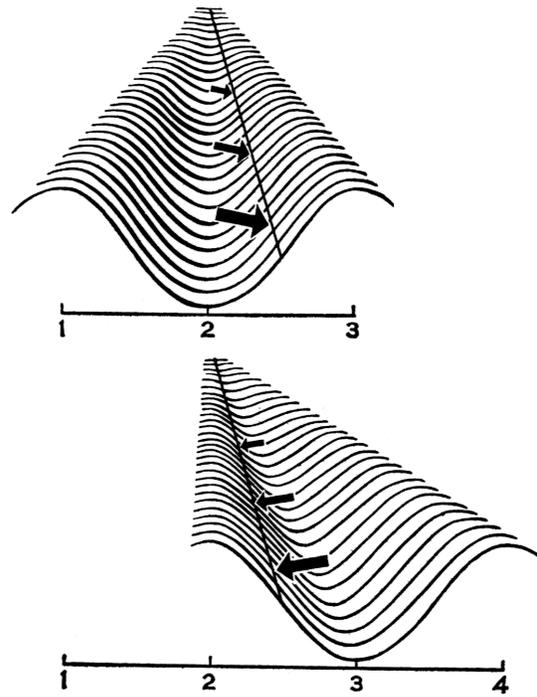


Figure 11

A Diagram of 'Genetic Assimilation,' from Conrad H. Waddington, *The Nature of Life* (London: Allen and Unwin, 1962), 95 (photo: author).

Genetic assimilation runs against neo-Darwinian common sense. Normally, the same set of genes would reliably create identical adult organisms (this is why there are identical twins and clones). These adults are then subject to natural selection. Because there is normally a direct relationship between genes and adult organisms, natural selection is essentially selecting for *genes*, with an adult acting as a proxy. Waddington uses images such as Figure 11 to help explain that, in some unusual cases, the developmental process that mediates between genes and adult characteristics cannot be ignored. Changing the developmental environment—shifting the landscape—can sometimes cause the same genes (represented by the black line) to be expressed in different ways (development “rolls” into a different “side valley,” leading to a different adult organism). In the context of the modern synthesis, this idea was heretical. Waddington argues that something only subtly different from phenomena known to be impossible—like the neck of a baby giraffe being longer because its parents stretched to reach leaves (the inheritance of acquired characteristics or “soft inheritance”)—is, in fact, possible.

Because he was operating in dangerous intellectual territory, Waddington was often accused of basic theoretical errors. Modern synthesis biologists later justified the exclusion of Waddington’s theories, which they acknowledged to be the “missing chapter” of the

synthesis, because everyone had “difficulty in explaining” them.⁴⁰ They seemed to exist in the questionable “borderline field of science and philosophy.” Waddington’s style matched the situation in which he found himself. Waddington adopted a direct, conversational style because he needed to provoke enough engagement from his colleagues for him to be able to explain his convoluted theories. Repeatedly in his writing he refers to “well-established” theoretical points that “we know,” but which have apparently been forgotten by the people around him. His shifting, contradictory descriptions of the epigenetic landscape should be seen as part of a conversation spanning decades between Waddington and his colleagues (or perhaps the institution of science more generally). Waddington proposed, elaborated, and abandoned metaphors as it suited the shifting conversational terrain; it was his complex and ambiguous images that allowed him to do this.

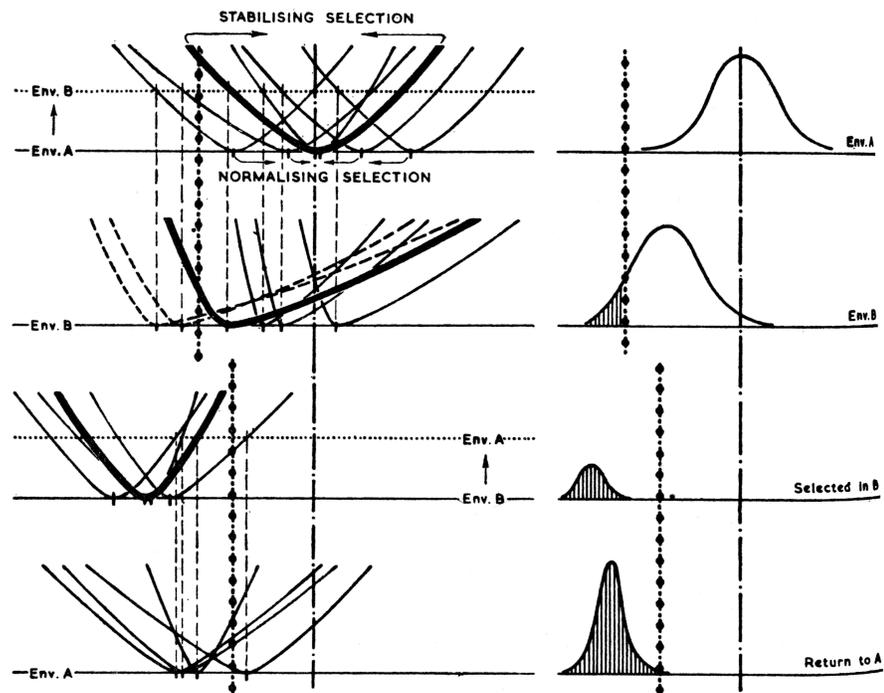


Figure 12

Normalising and Canalising (Stabilising) Selection and the Effects of Change of Environment, from Conrad H. Waddington, *The Strategy of the Genes* (London: Allen and Unwin, 1957), 76 (photo: author).

Some of Waddington’s illustrations require heroic feats of interpretation. Figure 12, for example, shows cross-sections of a morphing epigenetic landscape. In the accompanying text, Waddington walks his readers through each of these and related curves (e.g. Fig. 13) in terms of the biological events they depict, some of which implied heretical phenomena such as genetic assimilation.⁴¹ Another example is Figure 14, which shows the feedback loops that

⁴⁰ Viktor Hamburger, “Embryology and the Modern Synthesis in Evolutionary Theory,” in *The Evolutionary Synthesis: Perspectives on the Unification of Biology*, ed. Ernst Mayr and William B. Provine (Cambridge, MA: Harvard University Press, 1980), 110.

⁴¹ Waddington, *The Strategy of the Genes*, 76.

shape the epigenetic landscape.⁴² Waddington explains how the arrows in another diagram (Fig. 15), match up with one of these arrows.⁴³ Toggling conceptually between the cybernetic metaphor of the former diagram and the landscape metaphor of the latter is no mean feat.

Waddington's concepts have not gotten any easier to explain. Updated versions of these diagrams (e.g. Fig. 16) involve the same convoluted causality.⁴⁴ To engage with these diagrams and the concepts they explain, readers have to slow down and think their way carefully through a complicated theoretical terrain. Even the shortcomings of Waddington's images reveal key aspects of his theory.

Compelled by the Diagram

We can now see the efficacy of Waddington's particular visual practice. Waddington created a set of illustrations of a series of (contradictory) analogical models to condense a career-spanning theoretical conversation into a set of visual "proofs" that required unpacking, effectively drawing out the duration of his colleagues' engagement with his concepts. Waddington's diagrams focused and directed the conversation. They gave him and his colleagues something to ponder, something to talk about.

The effect of a compelling diagram, and why it is said to be *compelling*, begins with the capturing of a reader's attention. Historians of science have tended to downplay the importance of singular, compelling images. Bruno Latour sums up the reasoning: "One should not isolate the scientific imagery and shoehorn it into the types of questions raised by iconography. There is nothing visual in scientific visual imagery. Literally, there is nothing to be 'seen.'"⁴⁵ Latour and others argue that images are typically used by scientists as links in chains of reasoning, and that they are meaningless outside of these chains.⁴⁶ Latour makes one exception: the (in his view rare) case in which "one isolated image extracted out of the chains as 'the definitive proof' of the phenomenon they wish to describe," for "pedagogical purposes." I suggest that images are more often meant to be *seen* (and, more to the point, grappled with, thought through, and questioned) than Latour allows. Images can put a theoretical proposition "all in one place," rather than spread throughout a text. This *condensation* is a powerful feature. What Latour identifies as the "pedagogical" use of images is really the function of analogical models: to condense theories and multiply questions. And, analogical models are pervasive in scientific practice.⁴⁷ Illustrations such as Waddington's only work if the reader feels compelled to pause, look closely, and work through the details—that is, to pull the image momentarily out of the chain to which it belongs and to treat it iconographically.

⁴² Conrad Hal Waddington, *New Patterns in Genetics and Development* (New York: Columbia University Press, 1962), 7.

⁴³ Conrad Hal Waddington, *The Nature of Life*, (London: Allen and Unwin, 1961), 95.

⁴⁴ Kevin N. Laland et. al., "Cause and Effect in Biology Revisited: Is Mayr's Proximate-Ultimate Dichotomy Still Useful?," *Science* 334 (2011): 1515.

⁴⁵ Bruno Latour, "The More Manipulations the Better," in *Representation in Scientific Practice Revisited*, ed. Catelijne Coopmans et. al. (Cambridge, MA: MIT Press, 2014), accessed June 25, 2015, <http://www.bruno-latour.fr/sites/default/files/P-158-WOOLGAR-IMAGE.pdf>

⁴⁶ James Elkins makes a more refined version of this argument; James Elkins, "Introduction," in *Visual Practices Across the University*, ed. James Elkins (Munich: Wilhelm Fink, 2007). Emphasis original.

⁴⁷ For a related discussion of metaphors, see George Lakoff and Mark Johnson, *Metaphors We Live By* (Chicago: University of Chicago Press, 1980).

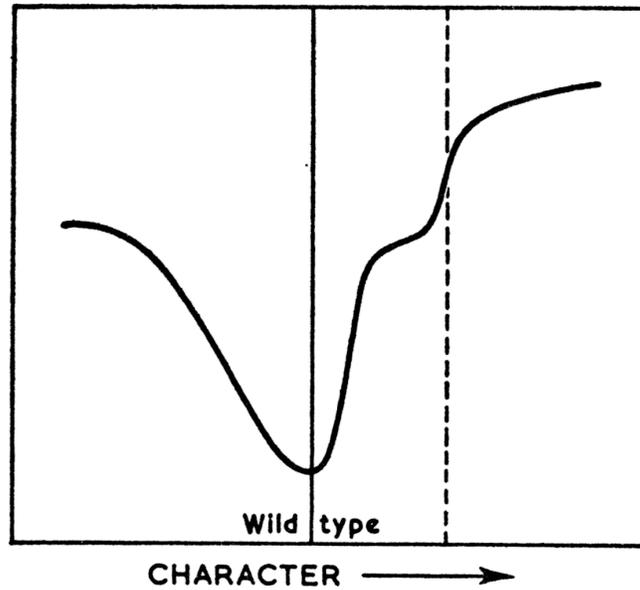


Figure 13

An Asymmetrical Canalisation Cross-Section, from Conrad H. Waddington, *The Strategy of the Genes* (London: Allen and Unwin, 1957), 128 (photo: author).

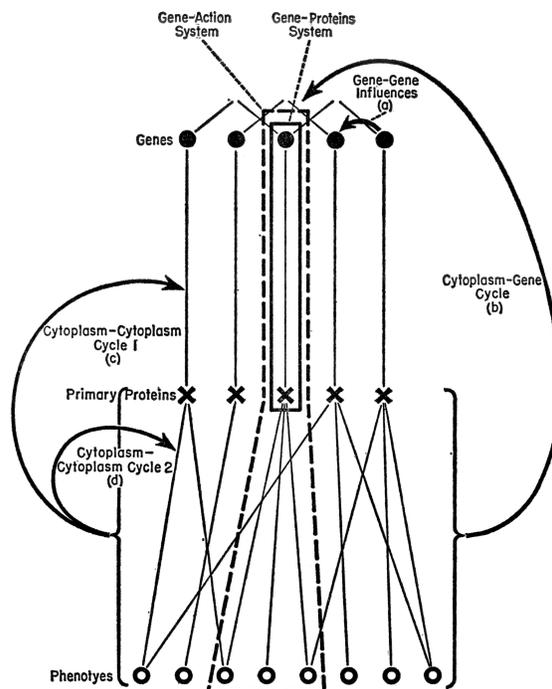


Figure 14

Epigenetic Action System of Cell, from Conrad H. Waddington, *New Patterns in Genetics and Development* (New York: Columbia University Press, 1962), 7 (photo: author).

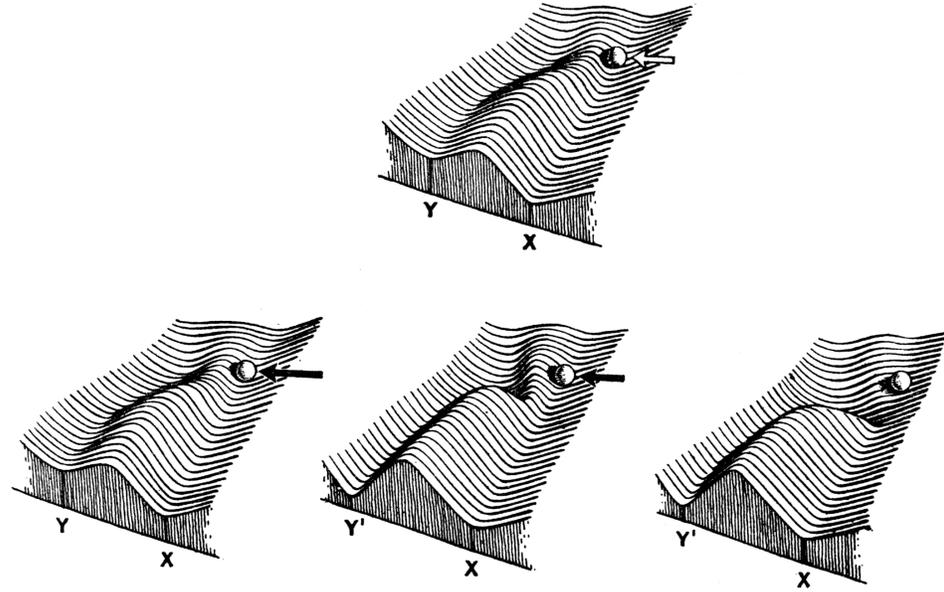


Figure 15

'Organic Selection' (the Baldwin Effect) and Genetic Assimilation, from Conrad H. Waddington, *The Strategy of the Genes* (London: Allen and Unwin, 1957), 167 (photo: author).

What makes an image or illustration or diagram *compelling*? Understanding this requires a description of what exactly is being seen and the cognitive work of seeing.⁴⁸ There are two dangers along this analytical route. First, the analyst may appear to be appreciating visual features for their own sake. Second, he may seem to be projecting his thoughts into another's head. I think these dangers are unavoidable and that the analytical results justify the means. Anthropologist Alfred Gell has gone further down this route than most. In his 1998 book, *Art and Agency*, Gell attempts to explain the cultural phenomenon of decorative patterning. Why put a complex pattern on a Persian rug? His answer is that the viewer feels a "pleasurable frustration" when trying to decipher the pattern.⁴⁹ Figuring out one part of the pattern (one figure/ground relationship, for example) means losing sight of another. The viewer is drawn into the pattern on the rug as she tries and fails to hold everything in mind at once. As Gell explains it, "We are drawn into the pattern and held inside it.... The pattern is a mind-trap...."⁵⁰ Trying to match up features of an illustration of an analogical model to concrete biological phenomena is a similarly frustrating, pleasurable, and productive mental exercise. Waddington's reason for putting complex diagrams in his books is not so different from the reason someone might want a decorative pattern on her rug: "the application of a decorative pattern to an artefact multiplies the number of its parts and the density of their

⁴⁸ Incidentally, these are exactly what Latour has suggested *not* doing, though his approach is becoming more pluralistic; see Bruno Latour, *An Inquiry into Modes of Existence* (Cambridge, MA: Harvard University Press, 2013).

⁴⁹ Alfred Gell, *Art and Agency: An Anthropological Theory* (Oxford: Clarendon, 1998).

⁵⁰ *Ibid.*, 80.

internal relationships."⁵¹ One final example from Gell, trying to understand a type of Indian chalk drawing (Fig. 17), describes the end result:

[E]ven if one 'knows' (intellectually) that this design is made up of four separate, but identical loops differently oriented, it is extremely frustrating to attempt to abstract individual loops from the overall design. ... Where simple geometric figures are concerned, 'seeing' (a triangle, say) is tantamount to mentally intending or projecting the construction of the figure, line by line. But this is impossible to do with complex figures like this kolam.⁵²

Analogously, when presented with a complex illustration of an analogical model, the viewer assumes, as a precondition of trying to decipher it, that the concept being represented makes sense. To decipher the illustration, she must feel compelled to close the gap between knowing that it means *something* and knowing exactly *what* it means (including the limits of this meaning). The process of deciphering may require the surrounding text, other illustrations, other concepts, other books, experimentation, and so on. The illustration, if it is compelling, serves as a focal point of this cognitive work.

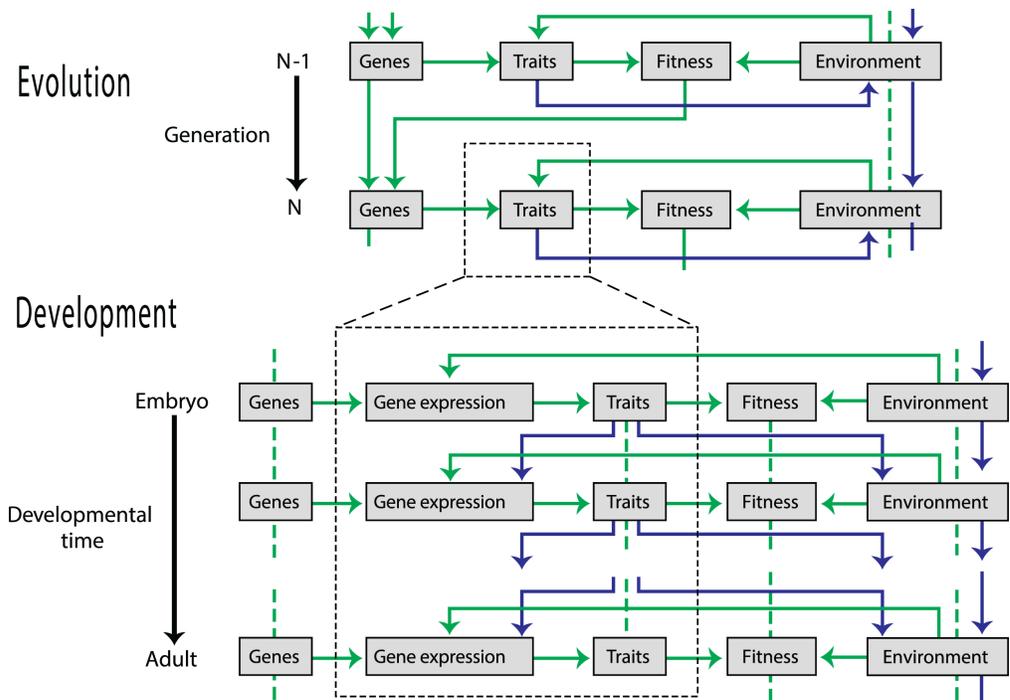


Figure 16

Matthew Allen, *Graphs Depicting the Causal Pathways Involved in the Evolution and Development of Traits: A Modern Developmental Perspective*, after the diagram published in Kevin N. Laland et al., "Cause and Effect in Biology Revisited: Is Mayr's Proximate-Ultimate Dichotomy Still Useful?," *Science* 224 (2011), 1513 (photo: author).

⁵¹ Ibid., 76.

⁵² Ibid., 85.

Waddington used a strategy that involved compelling diagrams because he was committed to the project of including all biological phenomena within a single theoretical system; this was the point of his late-career work on “theoretical biology.” He wanted biologists to be able to talk about genes, development, and evolution at the same time. Complex images helped him manage this process. Again, Gell describes the intention:

Patterns, by their multiplicity and the difficulty we have in grasping their mathematical or geometrical basis by mere visual inspection, generate relationships over time between persons and things, because what they present to the mind is, cognitively speaking, always ‘unfinished business.’⁵³

Waddington’s diagrams and concepts present biological phenomena as complex “patterns” that cannot be distilled into simple rules. Thinking of biology this way is a matter of style. Waddington’s distaste for pragmatic compromise and his preference for inconclusive conversations matched his visual practice.

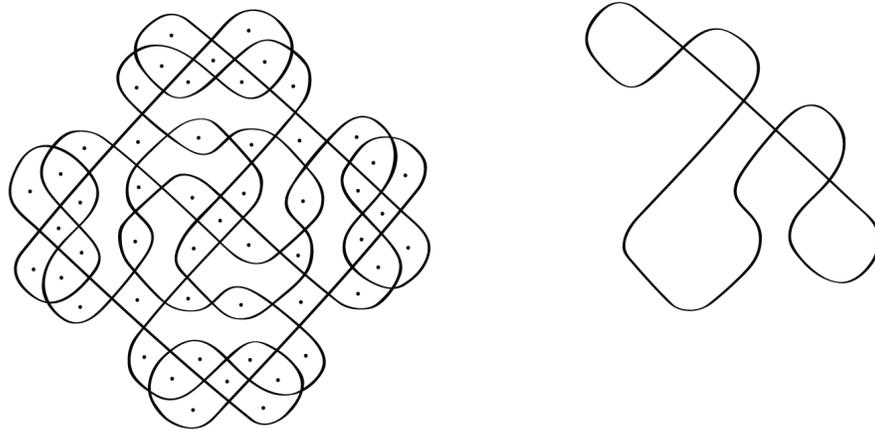


Figure 17

Matthew Allen, *Kolam Threshold Design: The Pattern as Topological Snare and The Constitutive Element of the Kolam*, after a diagram in Alfred Gell, *Art and Agency* (Oxford: Clarendon, 1998), 85 and 86 (photo: author).

Conclusion

Taken together, Waddington’s illustrations of the epigenetic landscape suggest an unusual type of synthetic project. While modern synthesis biologists produced a simple framework for dividing up biological knowledge, Waddington sought to bring all biological phenomena together in a way that does not always make immediate sense. He insisted that, in principle, nothing should be left out.

The legacy of logical positivism in analytical philosophy and history of science continues to privilege well-formed sentences, explicit argumentation, and conclusions that follow one another in a linear way. By contrast, a compelling illustration condenses a great deal of

⁵³ Ibid., 80.

conceptualization into a small, non-linear space. Sometimes Waddington's most important questions are raised by his illustrations. Looking again at a diagram of the epigenetic landscape (Fig. 1), the questions multiply. Where exactly is the embryo? What represents the cell? What is the role of time? What is the landscape itself, in biological terms? Because these questions are not always raised explicitly in the accompanying text and a satisfying answer may not exist, they may be ignored rather than thought through. Against explicit, step-by-step argumentation, Waddington favors the risky move of raising too many questions to answer. He gambles that biologists will not settle for simplified, straightforward explanations in the meantime.

In answer to the perennial question of whether images are necessary for science, I propose that images function effectively at drawing viewers in, confounding them, and prodding them to ask questions. Images are often thought of in science and technology studies as links in chains of reasoning, but images do not always play the role of providing positive bits of information. As I have shown here with Waddington's epigenetic landscape, sometimes images *get in the way* of knowledge by bringing up inconvenient complications and suggesting alternative interpretations. Compelling images draw out the process of understanding and help ensure that conclusions are not jumped to too quickly.

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