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Symmetry and the Explanation of Organismal Form

Commentary on Martin Golubitsky

1 Introduction

Golubitsky (this volume) presented three examples in which the concepts of symmetry and symmetry breaking, as well as their mathematical formalizations, played an important role in understanding patterns exhibited by physical and biological systems. These examples concerned patterns occurring in burner flames, in animal locomotion and in visual hallucinations. A striking feature of these examples was that the same general mathematical model of symmetry breaking could be applied in all cases, even though the systems under consideration came from quite different realms. Golubitsky's claims were that the mathematics of symmetry and symmetry breaking can help us understand the origins of patterns observed in physical as well as biological systems, and that there is a general "menu of patterns" that encompasses patterns that can be realized in materially very different kinds of systems (this volume; Stewart and Golubitsky, 1993: 186, 207, 218).

The philosophical question that Golubitsky's claims give rise to pertains to mathematical models in general: If there are general mathematical models that apply to materially very different kinds of systems, physical as well as biological ones, and can help us understand how these systems work, then what exactly is the role of such models in understanding and explaining the phenomena under study? What is the epistemic work that such models do in science?

This is a very broad question, which needs to be constrained more. Here, I will only consider one of Golubitsky's examples, namely the explanations of organismal traits such as the various locomotive patterns that animals exhibit. Where do mathematical models of the sort discussed by Golubitsky fit into the larger explanatory structure of biological science? I will begin by addressing the role of mathematical models in biology in general.

2 What work do mathematical models do in the biosciences?

Although mathematical models are widespread in biology, the role of mathematics in biology seems quite different from its role in, for example, physics and chemistry. In these latter sciences, mathematical formalisms constitute a core feature of theories and explanations. But this is not so for the principal theories of biology. For example, evolutionary theory and evolutionary explanations, which constitute the backbone of biological science,[1] are often presented in verbal/conceptual form without using much mathematics. Similarly, organismal development is usually explained in terms of the operation of different genes and gene networks without necessarily relying on mathematical formalisms. This is not to say that mathematics is unimportant in developmental and evolutionary biology: it is not (e.g., Rice, 2004), but it does play a less prominent role in biology than in the exact natural sciences. Accordingly, Ernst Mayr (1982: 43) once claimed that progress in biology does not occur by formulating strict laws of the sort found in the physical sciences, but is largely a matter of the articulation and refinement of concepts.

This suggests that mathematical models in biology do not play their main parts in the formulation of explanations. Rather, their main roles might be heuristic. They can aid communication and serve didactical and rhetorical purposes by functioning as metaphors and analogies that represent real systems in ways that are easier to understand than the complex "real thing" (e.g., Stewart, 2003: 184). Moreover, they enable scientists to simulate how systems behave under various conditions in cases in which the "real thing" is difficult to access.

Golubitsky's example of animal gaits supports this suggestion (this volume; Field and Golubitsky, 1992: 32; Stewart and Golubitsky, 1993: Chapter 8; Golubitsky et al., 1998; 1999; Stewart, 2003; Pinto and Golubitsky, 2006). There, models play two heuristic roles. First, they provide information about how individual animals realize locomotion, thus contributing to the study of how organisms work. According to a widely held (but not uncontroversial – Stewart and Golubitsky, 1993: 201–203) assumption, animal locomotion is controlled by so-called central pattern generators (CPGs), neural networks that control limb motion (Stewart and Golubitsky, 1993: 199–203; Golubitsky et al., 1998: 57; Golubitsky et al., 1999: 693; Stewart, 2003: 197; Pinto and Golubitsky, 2006: 475). CPGs themselves are difficult to study *in vivo* or *in vitro*, so investigators work

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[1] Allegedly, "nothing in biology makes sense except in the light of evolution" (Dobzhansky, 1964: 449; 1973: 125).

backwards and try to derive information about how CPGs function from observations about the patterns they produce. The models used by Golubitsky and co-workers start from observed symmetries in animal gaits and symmetry breakings that occur in transfers between gaits. From this, the possible structures of the underlying CPGs are inferred, guided by the thought that the observed symmetries and symmetry breakings must correspond to those that an abstract network of a limited number of nodes can produce. The observed symmetries thus allow inferences about the symmetries of the underlying networks: "symmetry can be used to infer a plausible class of CPG network architectures from observed patterns of animal gaits" (Golubitsky et al., 1999: 693). In turn, from the symmetries of these general network architectures possible gaits can be predicted and looked for in animals in nature.[2]

Second, the relations between the various models of animal gaits can be used as indirect evidence for possible evolutionary scenarios (Pinto and Golubitsky, 2006: 487; Stewart, 2003: 196). The number of steps required to get from one set of gaits to another can be interpreted as an indication of the number of steps that evolution must have taken on its way from a taxon exhibiting one set of gaits to a taxon exhibiting the other set. For example, the steps needed to get from the set of gaits characteristic of quadrupedal locomotion to the set for bipedal locomotion can be taken to indicate the steps taken in the evolution of bipedal organisms from quadrupeds. Thus, mathematical models can provide clues about the evolutionary distance between and evolutionary history of taxa.

In both these cases, the inference is toward a class of possibilities (a class of possible CPG structures and a class of possible evolutionary routes). The models provide clues about which architectures or routes are possible, but not about the *actual* architectures or routes involved and thus don't provide any concrete explanatory details. The question thus remains open whether mathematical models can be more than heuristic tools and might perform "proper" explanatory roles. I will address this question by considering the search for a theory of organismal form.

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2 Golubitsky's example of visual hallucinations works in the same manner (Bressloff et al., 2001: 323–326; Bressloff et al., 2002: 476–477). The question is which neural network architectures are required to produce the variety of geometrical patterns found in visual hallucinations. This is answered by relating the observed symmetries of hallucination patterns to the symmetries that a producing network must possess. In this way the *possible* architectures of the visual cortex area responsible for producing visual hallucinations are inferred from the *actual* patterns of observed hallucinations.

3 What natural selection does not explain

Among the principal questions of biological science are why we have the organismal diversity that we do (rather than a different diversity) and why the organisms we find around us have the traits they do, instead of other possible traits they might have exhibited (and that sometimes organisms of different species *do* exhibit). Ever since Darwin's work an important part of the answers to these questions is given in terms of natural selection. But it has long been clear that selection constitutes only part of the answer.

In the first place, not *all* organismal traits are necessarily explained by selection, as paleontologist Stephen Jay Gould and geneticist Richard Lewontin pointed out in their famous "spandrels" paper (Gould and Lewontin, 1979). They criticized a procedure commonly followed by biologists, namely to break organisms down into discrete traits and to propose a separate adaptive story for each trait. Each trait's presence is then explained as a consequence of some function that it performed in ancestral organisms, endowing these with a selective advantage over organisms not possessing the trait in question. The underlying assumption is that "natural selection [is] so powerful and the constraints upon it so few that direct production of adaptation through its operation becomes the primary cause of nearly all organic form, function, and behaviour" (Gould and Lewontin, 1979: 584–585). However, Gould and Lewontin argued, this assumption stands unsupported: many organismal traits might be correctly explained as products of evolution by means of natural selection, but not necessarily all or nearly all traits are. Other explanatory factors besides natural selection, such as constraints on organismal development, also play important roles and may outweigh the explanatory importance of selection. Thus, Gould and Lewontin argued in favor of a pluralistic approach to biological explanation in which a plurality of explanatory factors can be invoked when explaining biodiversity and organismal traits. As they pointed out (Gould and Lewontin 1979: 589), this is in line with Darwin's own view "that Natural Selection has been the main but not exclusive means of modification" (Darwin, 1859: 6).

Furthermore, even for traits that are correctly explained as products of natural selection, selection is only part of the answer. Selection explains the trait's *presence* and its adaptive aspects, but there is more to say. Soon after the publication of the *Origin of Species*, biologists have begun to criticize Darwin's theory for addressing the spread and persistence of traits through ancestor-descendant lineages but not being able to explain how these traits arise in the first place (see Reydon, 2011). The criticism, which is also voiced by some contemporary biologists (Fontana and Buss, 1994; Gilbert, 2000), is that even if natural selection can

cause the differential reproduction of organism types with varying traits, it needs material to work with: natural selection filters, but it does not create new traits.

These two criticisms constitute the motivation behind a tradition of work in biology aiming to develop a theory of the origins of organismal forms, where 'form' is understood broadly as encompassing the shapes of organisms as well as their other physical and behavioral traits. The theory sought after should explain the origins of organismal traits and complement the theory of selection, which explains their preservation and spread.

4 Growth and form: D'Arcy Thompson's project

A key figure in the quest for a theory of organismal form was zoologist D'Arcy Wentworth Thompson. In his *On Growth and Form*, Thompson developed the project of comparing organismal forms to forms and patterns found in non-living systems and understanding these as instances of the same phenomena. The central thought in Thompson's book is that the principal causes of organismal forms are physical forces, such that organismal traits should be explained by taking recourse to general physical and chemical principles rather than selection and adaptation. Thompson thought of natural selection as a mere filter that could not create evolutionary novelty and thus could not explain organismal form (Bonner, 1992: xvii).

In a famous example, he compared the shapes of jellyfish to the shapes that liquid drops assume when falling through other liquids and suggested that both phenomena might be susceptible to the same explanation (Thompson, 1942: 392–398). Jellyfish here are modeled as expanding drops of a fluid with a different density than the water in which they are immersed and the observed shapes are explained as consequences of the operation of the physical laws that govern the flow of fluids in fluids.[3] It is unclear, however, exactly how much explanatory work Thompson's mathematical models do. For instance, Thompson writes:

> [W]e may use a hanging drop, which, while it sinks, remains suspended to the surface ... [T]he figure so produced, in either case, is closely analogous to that of a medusa or jellyfish ... *It is hard to say how much or little all these analogies imply*. But they indicate, at the very least, how certain simple organic *forms might be naturally assumed by one fluid mass within another*, when gravity, surface tension and fluid friction play their part (Thompson, 1942: 395–398; emphasis added).

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3 Note that another of Thompson's (1942: 39–50) examples concerned animal locomotion and flight.

Although Thompson was careful not to imply too much, this quotation does suggest that he took the analogy as having *some* explanatory value in that the various shapes of jellyfish can be explained as what is bound to occur for particular fluids under particular conditions.

Similarly to Golubitsky's models, Thompson's models take recourse to physical laws to map out the spectrum of what is possible under various conditions (Bonner, 1992: xxii). In this respect, the laws of physics function in the same way in explanations of organismal form as in explanations of phenomena in the non-living realm: in both cases there are general physical principles that apply universally and determine what is bound to occur in such-and-such kinds of systems under such-and-such conditions, irrespective of the systems' material bases. As Thompson writes at the end of his book: "So the living and the dead, things animate and inanimate ... are bound alike by physical and mathematical law" (Thompson, 1942: 1097).

This motif is found elsewhere too. For example, zoologist Rupert Riedl remarked that "[t]he living world happens to be crowded by universal patterns of organization which ... find no direct explanation through environmental conditions or adaptive radiation, but exist primarily through universal requirements which can only be expected under the systems conditions of complex organization itself" (Riedl, in Gould and Lewontin, 1979: 594). In a similar spirit, mathematician (and frequent collaborator of Golubitsky's) Ian Stewart remarked about the observed symmetry breakings in the developmental cycle of the alga *Acetabularia acetabulum* that these are the same as found in a particular type of fluid flow, "*as they should be* since such patterns are universal in cylindrically symmetric systems" (Stewart, 2003: 190; emphasis added). And it seems to me to be the motif underlying Golubitsky's suggestion that there is a general "menu of patterns" that can be realized in materially very different kinds of systems found in different realms in nature (this volume; Stewart and Golubitsky, 1993: 186, 207, 218).

Invoking such universal patterns that can be captured in mathematical models of symmetry and symmetry breakings does not explicate what is *actually* the case in a system under study, as it abstracts away from the system's characteristics. It narrows down the set of possible explanations of the phenomenon under study to a limited number of possible scenarios. On some accounts of explanation this could be accepted as "proper" scientific explanation and Thompson's and Golubitsky's models would count as "how possibly" explanations (O'Hara, 1988; Brandon, 1990; Resnik, 1991; Reiner, 1993). However, whether "how possibly" explanations should be accepted as "proper" scientific explanations is still a controversial issue in the philosophy of science.

5 Conclusion

As Golubitsky showed, symmetry breaking is common in the living world, e.g., in animal locomotion or organismal growth.[4] In Thompson's project, too, the concept of symmetry played an important role: "In all cases where the principle of maxima and minima comes into play [...] the configurations so produced are characterized by obvious and remarkable *symmetry*. Such symmetry is highly characteristic of organic forms and is rarely absent in living things" (Thompson, 1942: 357). If this is right, there clearly must be epistemic work to do for the concepts of symmetry and symmetry breaking and their mathematical formalizations in explanations of organismal form. But there are good reasons to think of this work as not being explanatory in and by itself.

Even though mathematical models of symmetry and symmetry breaking seem to provide "how possibly" explanations, the mathematics *itself* does not provide explanatory force: the applicable physical laws and system specifications do (cf. Stewart, 2003: 191). Similarly, symmetry breaking itself does not explain much. The explanatory work is done by the causes *underlying* symmetry breakings, i.e., the physical laws that govern particular kinds of systems and the slight imbalances in an overall symmetrical system that at some point causes the breaking of its symmetry (Stewart, 2003: 188). That the same mathematical model applies to a number of very different systems merely indicates that in all these systems the same physical laws are involved. Mathematical models of symmetries and symmetry breakings do not capture the complexity of the systems under study, but abstract away from much detail, allowing us to focus on the relevant overall patterns and to identify the relevant underlying laws. While this is important to gain insight into what could occur in the system under consideration, actual explanations of concrete phenomena will need to specify the details of the system itself.

Golubitsky's examples showed how models of symmetries and symmetry breakings provide clues about what might possibly be the case in the systems under study. The models describe how organismal function, development and evolution are constrained by the general laws of physics and chemistry, making some traits possible and others impossible (cf. Stewart, 2003: 200). One might interpret such models as adding "how possibly" explanations to the "how and why actually" explanations of functional, developmental and evolutionary biology. But in my view their role in fact is more heuristic in nature and it is to be doubted whether such "how possibly" explanations should count as "proper" scientific explanations on an equal level with other explanations in biology.

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4 Another example: non-spherically-symmetrical starfish develop from spherically symmetrical eggs (Field and Golubitsky, 1992: 32).

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