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Patterns in Physical and Biological Systems

Mathematics can be applied in many ways in science, but let's begin by focusing on one typical caricature. Study an application until it is possible to derive a detailed mathematical model. Then use mathematics (by which we include both analysis and computation) to solve that model and make predictions. Compare the results of the model with experiments; if there is a discrepancy refine the model and iterate the process. Spectacularly successful examples of this caricature include the n-body problem (a model for planetary motion) and the Navier-Stokes equations (a model for fluid motion) – though there are many other examples.

The question that we want to discuss here is what happens when a model is too complicated to be analyzed or when no detailed model can be derived. Can mathematics still be used to help understand that application and even to make predictions? The answer is yes – but one must ask the right kind of question.

The common approach is to understand the structure that a detailed model must have and then use that structure to make predictions about the kinds of solutions one can expect the unknown equations to produce. In the past 50 years this meta-principle has appeared in a number of different guises including, for example, catastrophe theory (R. Thom, 1972; E.C. Zeeman, 1977), bifurcation theory (J. Guckenheimer and P. Holmes, 1983; M. Golubitsky and D.G. Schaeffer, 1985), and symmetry-breaking and pattern formation (L. Michel, 1972; D.H. Sattinger, 1979; M. Golubitsky et al., 1988; M. Golubitsky and I. Stewart, 2002). In these theories some structure is assumed and then the kinds of solutions consistent with that structure are classified. Also, in these theories new solutions are found by classifying typical transitions as parameters are varied.

For example, catastrophe theory classifies the expected transitions between critical points as parameters are varied (assuming that the model has a potential function) and bifurcation theory classifies the expected kinds of dynamics that occur in systems of differential equations near an equilibrium that loses stability as a parameter is varied. In both theories the expected transitions depend on the number of (independent) parameters that the model is assumed to have. In symmetry-breaking and often in pattern formation the additional assumed structure is a group of symmetries for the model equations.

This article will focus on symmetry-breaking and pattern formation in its simplest form. We will discuss two applications where no detailed system of model equations is known, but where a group of symmetries for these unknown equations can safely be assumed. We will assume that there is a homogeneous (or

group invariant) equilibrium and classify the symmetry properties of new solutions when that equilibrium loses stability (a symmetry-breaking bifurcation) as a single parameter is varied. And then – we will interpret these results for the application. The focus will be on applications and predictions; only references will be given for the needed mathematics. Our exposition will follow closely the descriptions of these applications given in *The Symmetry Perspective* by (M. Golubitsky and I. Stewart, 2002) (indeed some of the material is taken verbatim from this volume). This reference also supplies many of the mathematical details behind the arguments that we give here.

1 Patterns in Flames

There is a huge literature on patterns in a variety of classical fluid dynamical and chemical reacting systems including the Taylor-Couette experiment, Bénard convection, the Faraday experiment, and the Belouysov-Zhabotinskii reaction. See, for example, the references in (M. Golubitsky and I. Stewart, 2002). An experimental system that has received somewhat less discussion is the pattern-rich porous plug burner studied for many years by the physicist Michael Gorman at the University of Houston (M. Gorman et al., 1994a,b).

A cross-section of Gorman's system is shown in Figure 1 (left). Viewed from above the burner is circularly symmetric. The flame is ignited on top of the burner and maintained by the fuel flowing continuously through the burner. A typical steady flame pattern is also shown in Figure 1 (right).

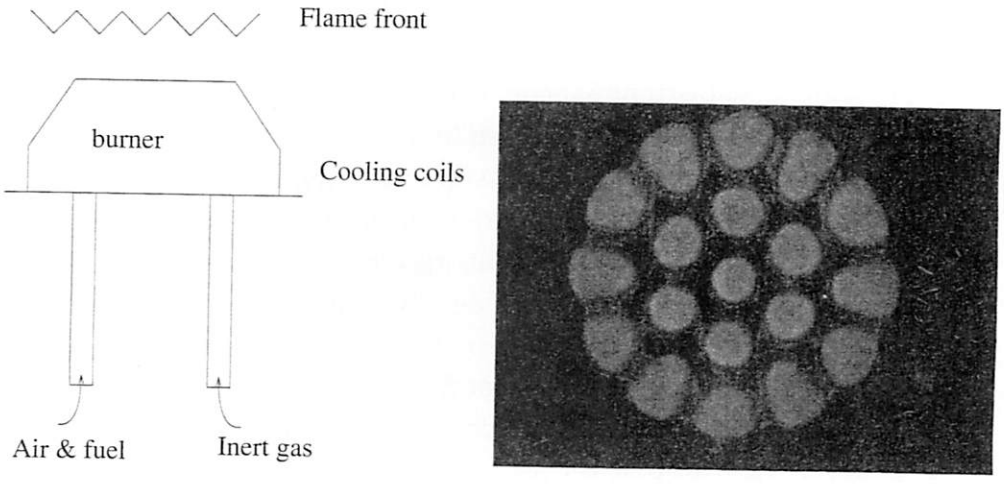

Figure 1: Cross section of a porous plug burner and a typical pattern formed by the flame on the burner's top surface. Images courtesy of M. Gorman.

Symmetry enters the discussion of flames most prominently through time-periodic states. A theorem that has been proved many times in the literature in specific applications, but whose validity depends only on the existence of circular symmetry (M. Golubitsky et al., 1988), is the following. When a circularly symmetric equilibrium of a circularly symmetric system (see Figure 2 (left)) loses stability to time-periodic oscillations two states form: rotating waves and standing waves. A *rotating wave* is a state whereby time evolution of the state is given by rigid rotation and a *standing wave* is a time-periodic state that has at least one line of symmetry for all time. The physical implication is that when a rotating wave is found in an experiment, it can be presumed that standing waves are also present; hence it is not surprising that the standing waves will also be observed.

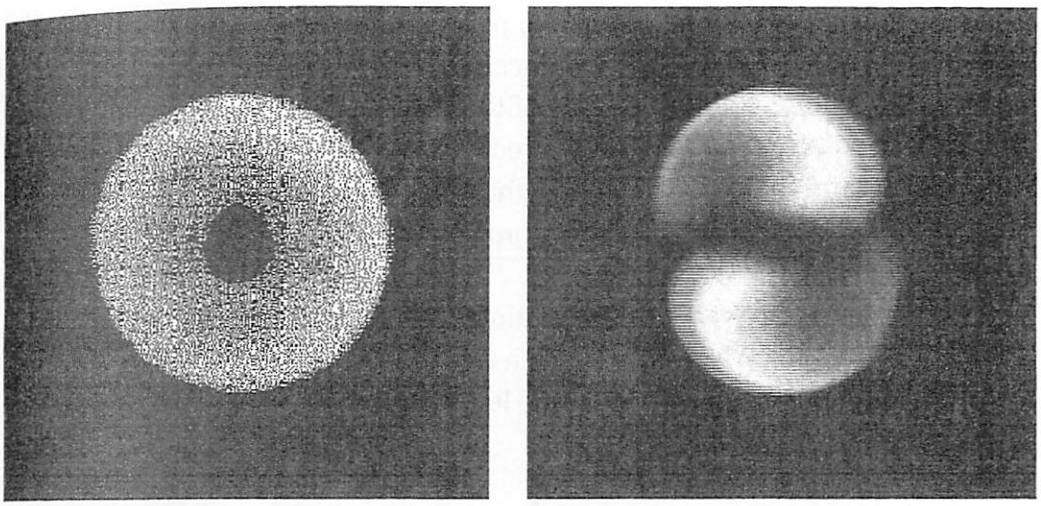

Figure 2: Flames on circular burner. (Left) Circularly symmetric flame; (right) rotating two-cell flame. Images courtesy of M. Gorman.

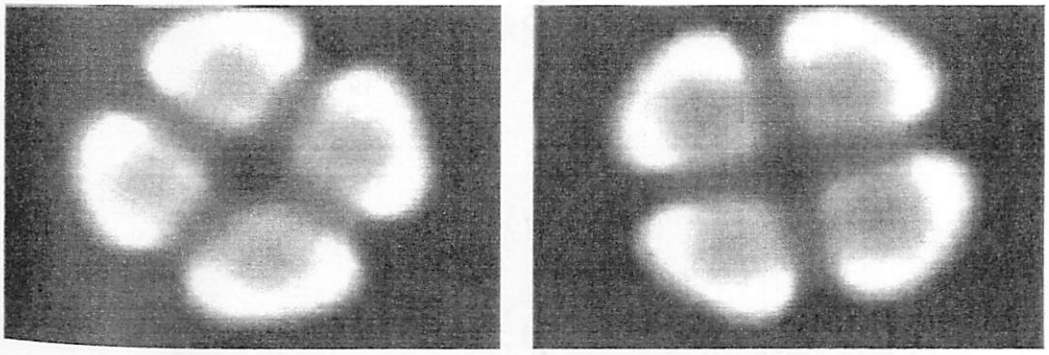

Figure 3: Standing wave flames on circular burner. Two images on one trajectory illustrating same four lines of symmetry. Images courtesy of M. Gorman.

This is precisely what Gorman found. He observed a rotating wave in the flame experiment (see Figure 2 (right)) and sometime later (a year or so, as it happened) Gorman also found the standing wave (see Figure 3).

2 Quadruped Central Pattern Generators

It is well known that all horses walk and that some horses trot while others pace. In addition squirrels bound and deer will sometimes pronk. There is one feature that is common to all gaits: they are repetitive; that is, they are time-periodic.

In the pace, trot, and bound the animal's legs can be divided into two pairs – the legs in each pair move in synchrony, while legs in different pairs move with a half-period phase shift. The two pairs in a *bound* consist of the fore legs and the hind legs; the two pairs in a *pace* consist of the left legs and the right legs; and the two pairs in a *trot* consist of the the two diagonal pairs of legs. The quadruped *walk* has a more complicated cadence (each leg moves independently with a quarter-period phase-shift in the order left hind, left fore, right hind, and right fore), whereas the quadruped *pronk* is a simple motion (all four legs move synchronously).

We summarize the descriptions of these five gaits in Figure 4 by indicating the phases in the gait cycle when each given leg hits the ground. For definiteness, we start the gait cycle when the left hind leg hits the ground.

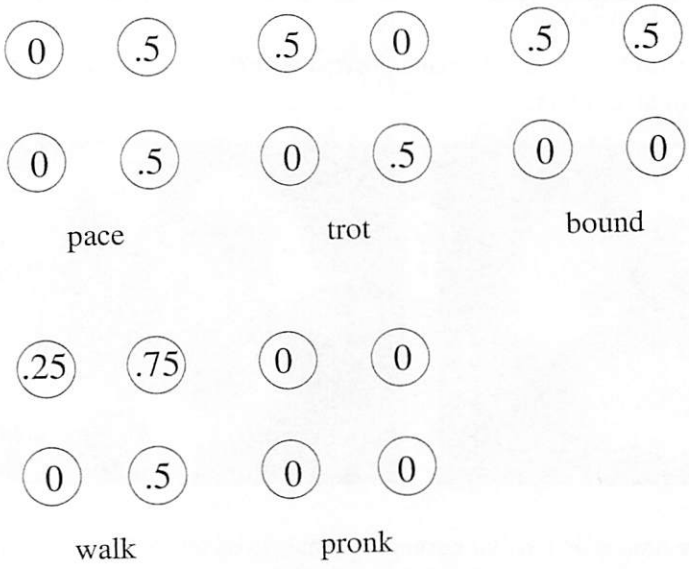

Figure 4: Five standard quadrupedal gaits.

(J.J. Collins and I. Stewart, 1993, 1994) and (G. Schöner et al., 1990) made the observation that each of these gaits can be distinguished by symmetry in the following sense. Spatio-temporal symmetries are permutations of the legs coupled with time shifts. So interchanging the two fore legs and the two hind legs of a bounding animal does not change the gait, while interchanging the two left legs and the two right legs leads to a half-period phase shift. In a walk permuting the legs in the order left hind to left fore to right hind to right fore leads to a quarter-period phase shift. Based on these gaits we consider three symmetries: the bilateral symmetry that simultaneously interchanges left legs and right legs; the transposition that interchanges front and back legs; and the walk symmetry. Table 1 lists which of these symmetries are applicable to each gait and, if applicable, the associated phase shift.

Table 1: Phase shifts corresponding to leg permutation symmetries in standard quadrupel gaits

Gait	left-right	front-back	walk
trot	1/2	1/2	n.a.
pace	1/2	0	n.a.
walk	1/2	n.a.	1/4
bound	0	1/2	1/2
pr̈onk	0	0	0

Biologists often make the assumption that somewhere in the nervous system is a locomotor *central pattern generator* or CPG that produces the rhythms associated to each gait. CPGs are known to exist in primitive animals but they have not been identified in mammals. Nevertheless, suppose we assume that there is a locomotor CPG in quadrupeds – how can we model it? Neurons themselves are modeled by systems of differential equations (for example, the Hodgkin-Huxley equations (J. Keener and J. Sneyd, 1998)) and CPGs are thought to be a coupled array of neurons (see (N. Kopell and G.B. Ermentrout, 1988, 1990), (G. Schöner et al., 1990), (R.H. Rand et al., 1988)). So we may assume that our model is (a perhaps large dimensional) system of coupled ODEs. What structure may we assume that such a system of equations should have?

We imagine that for each leg there is a single group of neurons whose job is to signal that leg to move, and that the groups of neurons are otherwise identical. Moreover, we assume that the groups of neurons are coupled in some manner – and to simplify matters we assume that the kinds of coupling fall into a small number of identical types. A natural mathematical question now arises – even at this level of generality. Can couplings between these four groups of neurons be

set up so that periodic solutions having the rhythms associated with each of these gaits exist? The answer is, perhaps surprisingly, no. The reason for this is subtle. It is known that trot and pace are different gaits. However, if a four group system were capable of producing periodic solutions with the symmetries of walk, trot, and pace, then walk and trot must be the same up to symmetry and would for all practical purposes be the same gait.

The next simplest model would have eight groups of neurons with each leg receiving signals from two different groups of neurons. (M. Golubitsky et al., 1998) introduced the network shown in Figure 5 by assuming that the eight-node network should independently have both bilateral κ symmetry and the four-cycle walk symmetry ω. Thus the symmetry group of the eight-cell quadruped CPG is $\Gamma = \mathbf{Z}_2(\kappa) \times \mathbf{Z}_4(\omega)$. For expository purposes we assume that cells 1, ... , 4 determine the timing of leg movements, and refer to the remaining four cells as 'hidden'. We also follow (M. Golubitsky et al., 1999) and show how the mathematical analysis of the structure of this CPG network can still lead to testable predictions about the structure of gaits.

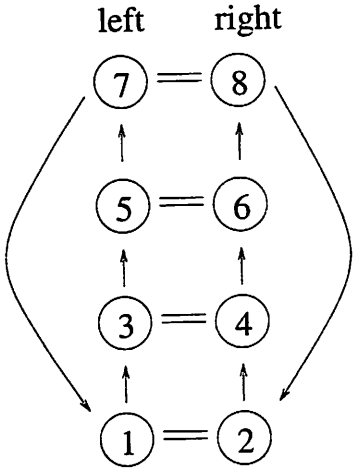

Figure 5: Eight-cell network for quadrupeds. Double lines indicate contralateral coupling; single lines indicate ipsilateral coupling. Direction of ipsilateral coupling is indicated by arrows; contralateral coupling is bidirectional.

In fact, the eight-cell network in Figure 5 (right) is essentially the only one that can produce periodic solutions with the spatio-temporal symmetries of walk, trot and pace (M. Golubitsky et al., 1998, 1999; P.L. Buono and M. Golubitsky, 2001). Next we ask the question: Which periodic solution types can be expected to emanate from a stand equilibrium in systems of differential equations associ-

ated with this cell network. We call these gait types *primary* gaits. It turns out that such systems can produce a non-standard gait in addition to the five gaits we have discussed previously. This gait is called the *jump* and can be described as 'fore feet hit ground, then hind feet hit ground after one beat, then three beats later fore feet hit ground'. The existence of this quadruped gait is a prediction of the model.

Indeed, we observed a gait with that spatio-temporal pattern of the jump at the Houston Livestock Show and Rodeo. Figure 6 shows four equal time-interval video frames of a bucking bronco. The timing of the footfalls is close to 0 and 1/4 of the period of this rhythmic motion. Later on we found that (P.P. Gambaryan, 1974) had identified the *primitive ricocheting jump* of a Norway rat and an Asia Minor gerbil that also has the cadence of the jump.

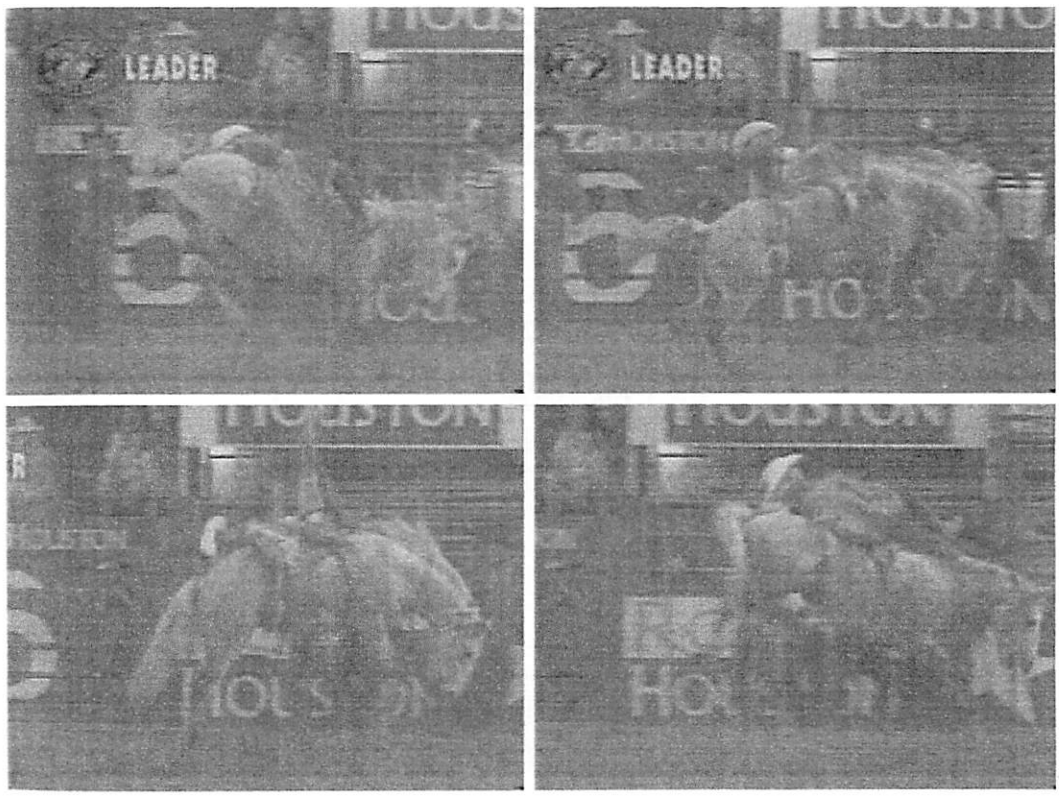

Figure 6: Approximate quarter cycles of bareback bronc jump at Houston Livestock Show and Rodeo.

3 Geometric Visual Hallucinations

(H. Klüver, 1966) observed that geometric visual hallucinations divide into four *form constants*: tunnels and funnels; spirals; lattices including honeycombs and phosphenes; and cobwebs. See Figure 7. (P.C. Bressloff et al., 2001, 2002) are able to explain the origins of the four form constants as symmetry-breaking with respect to the Euclidean group of planar translations, rotations and reflections as it acts on the primary visual cortex (V1). In this section we will describe that action.

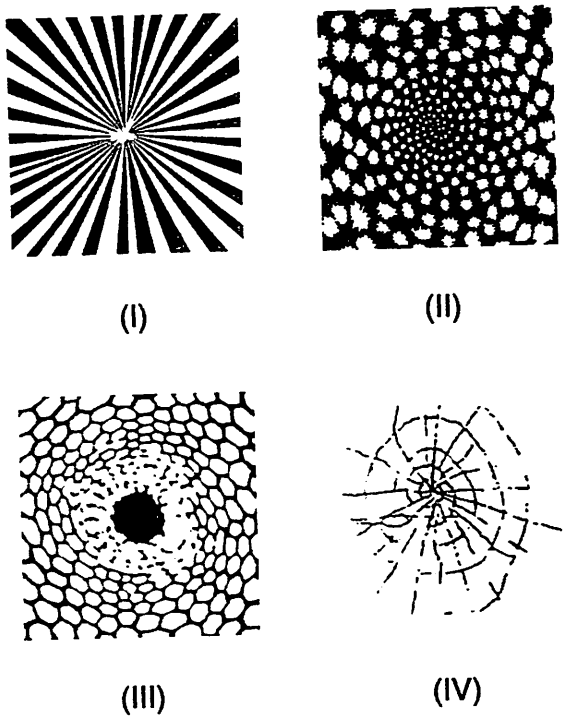

Figure 7: Hallucinatory form constants. (I) funnel and (II) spiral images seen following ingestion of LSD (R.K. Siegel and M.E. Jarvik, 1975), (III) honeycomb generated by marihuana (J. Clottes and D. Lewis-Williams, 1998), (IV) cobweb petroglyph (A. Patterson, 1992).

The idea of viewing the origin of geometric visual hallucinations dates to the work of (G.B. Ermentrout and J.D. Cowan, 1979). Ermentrout and Cowan argue that when an individual is under the influence of a drug, the entire primary visual cortex is stimulated uniformly by the drug and not by the retina. When this forced stimulus is sufficiently large, patterns of activation are formed on V1 and interpreted by the brain as visual images – often with a distinctly geometric flavor. However, the work in (G.B. Ermentrout and J.D. Cowan, 1979) was completed

before the nature of coupling of neurons in V1 was understood. Thus (G.B. Ermentrout and J.D. Cowan, 1979) assumed that models of V1 are Euclidean-invariant with respect to the standard action of the Euclidean group on the plane and symmetry-breaking arguments only led to two of the four form constants (funnels and spirals).

In this section we present part of the discussion of V1 in (M. Golubitsky and I. Stewart, 2002) (much of it verbatim), which itself is an abbreviated version of the discussion in (P.C. Bressloff et al., 2001). In mammalian vision, neurons in V1 are known to be sensitive to the orientation of contours in the visual field. Moreover, as discussed in (P.C. Bressloff et al., 2001), the pattern of neuronal connections in V1 leads to a specific action of the Euclidean group that is different from the standard one on the plane.

The V1 layer is approximately a square, $40mm$ on a side. (D.H. Hubel and T.N. Wiesel, 1974a,b,c) noted that V1 is divided into small areas of about $1mm$ diameter, called *hypercolumns*, and the neurons in each hypercolumn receive signals from one small area in the retina. A hypercolumn contains all cortical cells that correspond to such an area: its architecture allows it to determine whether a contour occurs at that point in the retinal image, and if so, what its orientation is. This task is accomplished by having all pairs of cells in a hypercolumn connected by inhibitory coupling – so if a contour is detected by one neuron, it tends to suppress the other neurons in that hypercolumn, a local *winner-take-all* strategy. Experimental confirmation of the existence of hypercolumns is found in (G. G. Blasdel, 1992), see the iso-orientation patches in Figure 8.

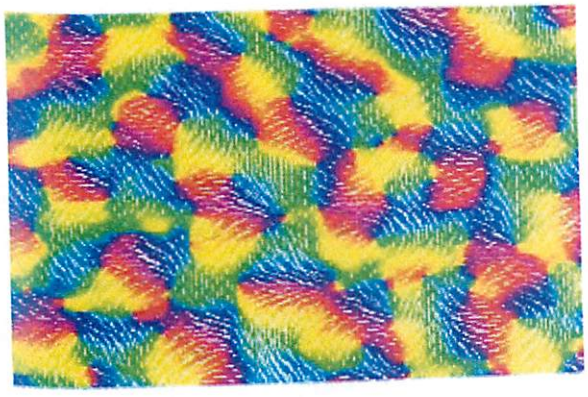

Figure 8: Distribution of orientation preferences in V1 obtained via optical imaging. Redrawn from (G. G. Blasdel, 1992).

What is curious – and crucial from the symmetry point of view – is how hypercolumns themselves are coupled. In recent years information has been obtained

about connections using, for example, optical imaging with voltage-sensitive dyes (W.H. Bosking et al., 1997). These studies show that cells that selectively fire for one orientation make contact only every millimeter or so along their axons with cells that fire selectively in the same orientation. See Figure 9, which illustrates the inhomogeneity in lateral coupling.

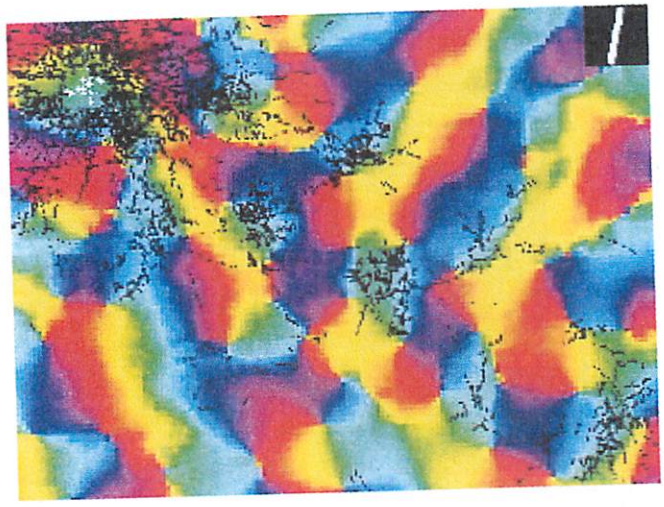

Figure 9: Lateral connections made by a cell in V1 superimposed on iso-orientation patches. Redrawn from (W.H. Bosking et al., 1997).

In addition, it appears that the long axons that support such connections, known as *intrinsic lateral* or horizontal connections, tend to be oriented more or less along the direction of their cells' preference. See the schematic diagram in Figure 10. Note that the strength of the lateral connection between hypercolumns is small when compared to the strength of the local connections within hypercolumns. These observations lead to the schematic pattern of neuronal connections shown in Figure 10.

Observe that when one makes the hypercolumns infinitesimal then the resulting schematic is invariant under translations but that rotations spoil the form of the lateral connections unless the orientation tuning of neurons within a hypercolumn is also relabeled (by the amount of rotation). So the Ermentrout-Cowan and the Bressloff-Cowan models both have Euclidean symmetry, but the ways that the Euclidean group acts are different and this leads to different pattern formation results. The end result is that the Bressloff-Cowan model predicts planforms of the type in Figure 11. Note the similarities with the geometric hallucinations reported in Figure 7.

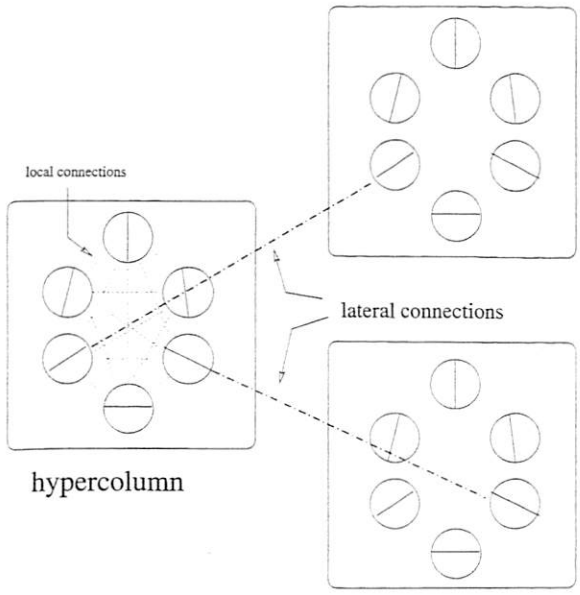

Figure 10: Short and long range connections in the visual cortex. · · · inhibitory; · – · – · – excitatory.

4 Conclusions

We have attempted to show how the existence of symmetry (both in equilibrium and time-periodic states) can help to understand patterns in applications even when the application has no precise mathematical model.

The symmetry description of locomotor central pattern generators leads to a variety of predictions about quadrupedal and bipedal gaits. In this article we described only one: the existence of an unexpected but natural gait – the jump. The proposed structure of CPG models leads to a variety of other predictions (the difference between primary and secondary gaits; the physiological need for each leg to be controlled by two neuron groups; and unexpected properties of centipede primary gaits). See (M. Golubitsky et al., 1999; M. Golubitsky and I. Stewart, 2002).

The symmetry of the primary visual cortex (determined experimentally) led, through symmetry-breaking arguments, to an unexpected correlation between this symmetry and the richness of geometric visual hallucinations. It is important to observe that this correlation can be understood without the need of a detailed model of the cortex V1 – just the symmetry structure that such a model should have.

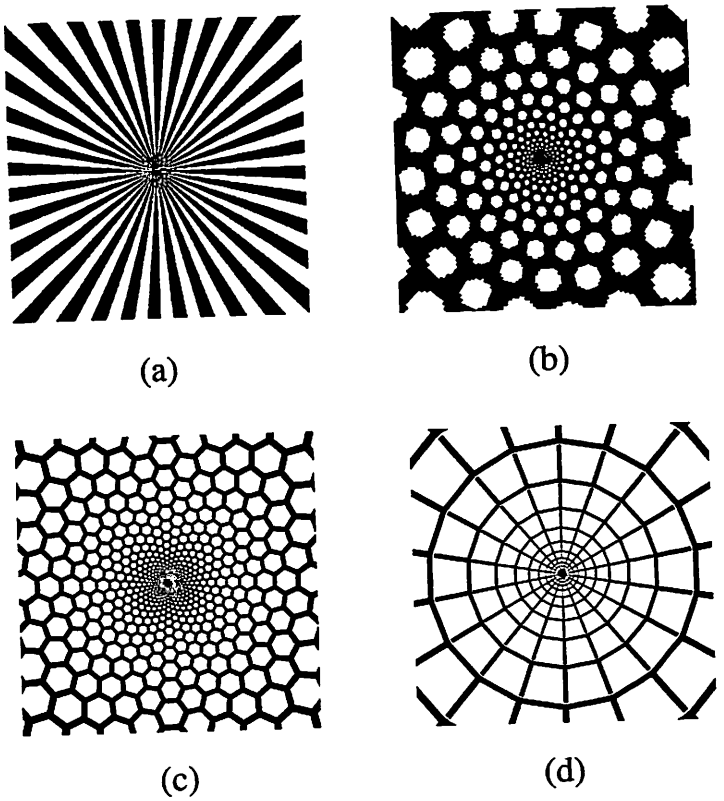

Figure 11: Taken from Bressloff et al. 2002

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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

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 coworkers 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.

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).

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.

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

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