Martin Golubitsky

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).

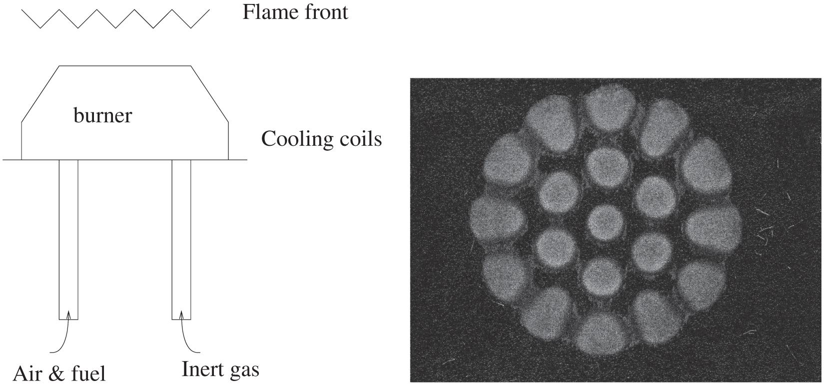


Figure 1: Cross section of a porous plug burner and a typical pattern formed by the flame on the burner's top surface. Images courtesy of M. Gorman.

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.

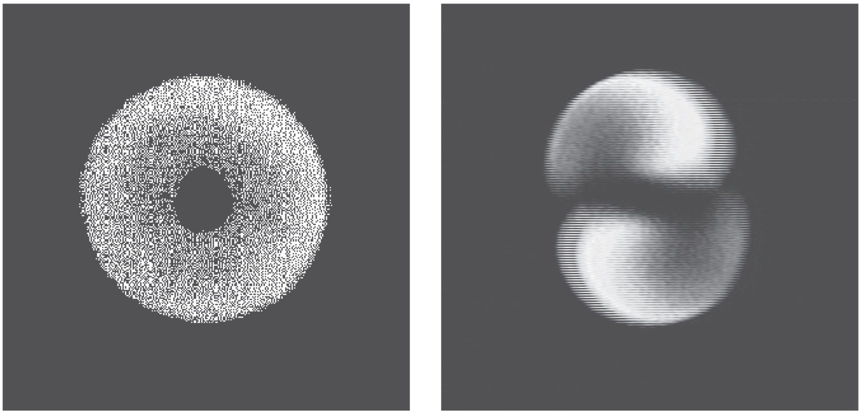


Figure 2: Flames on circular burner. (Left) Circularly symmetric flame; (right) rotating two-cell flame. Images courtesy of M. Gorman.

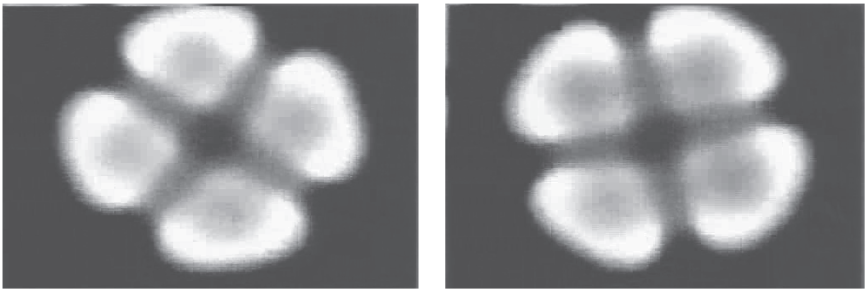


Figure 3: Standing wave flames on circular burner. Two images on one trajectory illustrating same four lines of symmetry. Images courtesy of M. Gorman.

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.

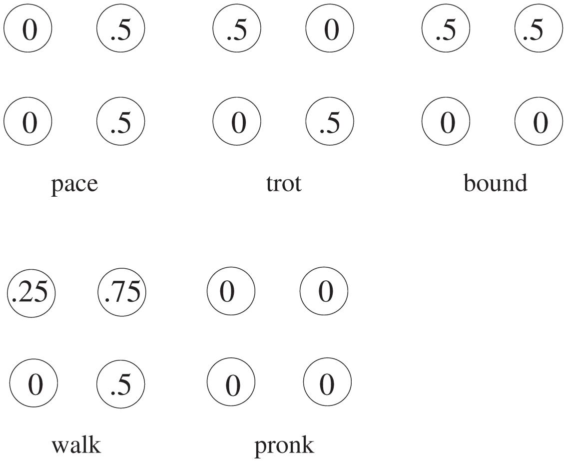


Figure 4: Five standard quadrupedal gaits.

(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
pronk	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.

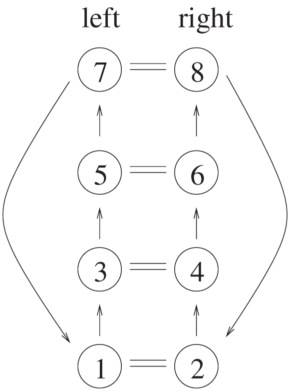


Figure 5: Eight-cell network for quadrupeds. Double lines indicate contralateral coupling; single lines indicate ipsilateral coupling. Direction of ipsilateral coupling is indicated by arrows; contralateral coupling is bidirectional.

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 associated 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.

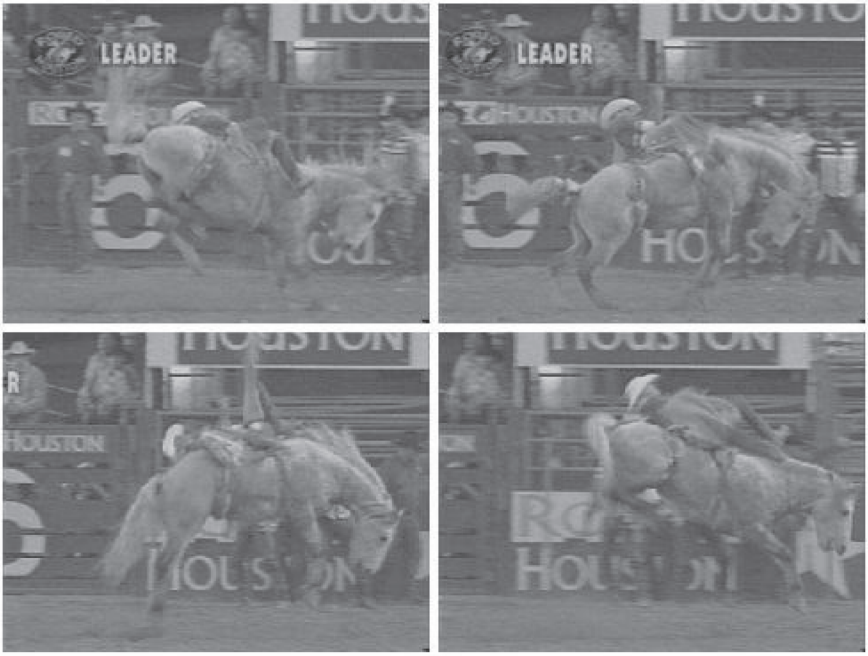


Figure 6: Approximate quarter cycles of bareback bronc jump at Houston Livestock Show and Rodeo.

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.

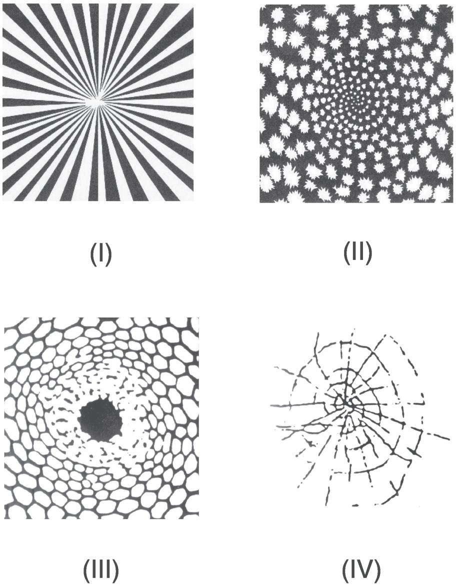

(I) (II)
(III) (IV)

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.

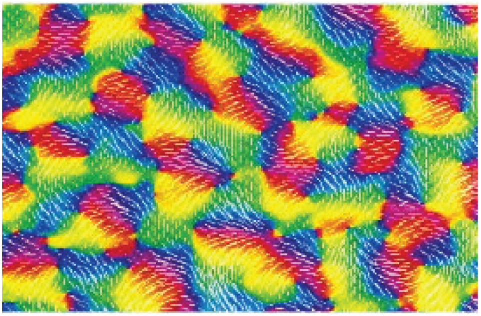


Figure 8: Distribution of orientation preferences in V1 obtained via optical imaging. Redrawn from (G. G. Blasdel, 1992).

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.

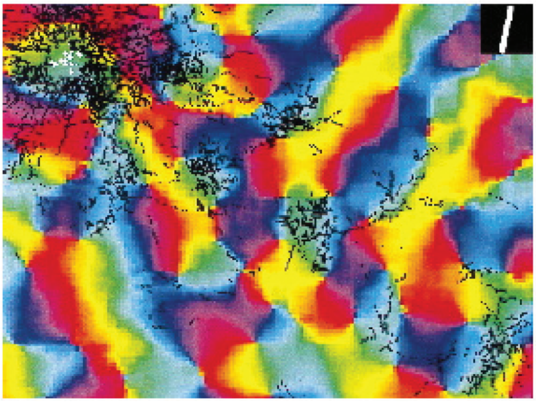


Figure 9: Lateral connections made by a cell in V1 superimposed on iso-orientation patches. Redrawn from (W.H. Bosking et al., 1997).

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.

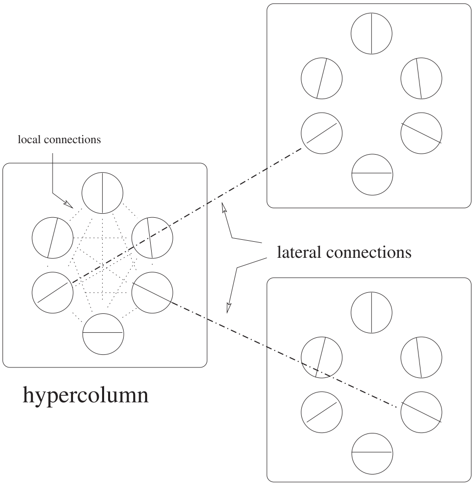


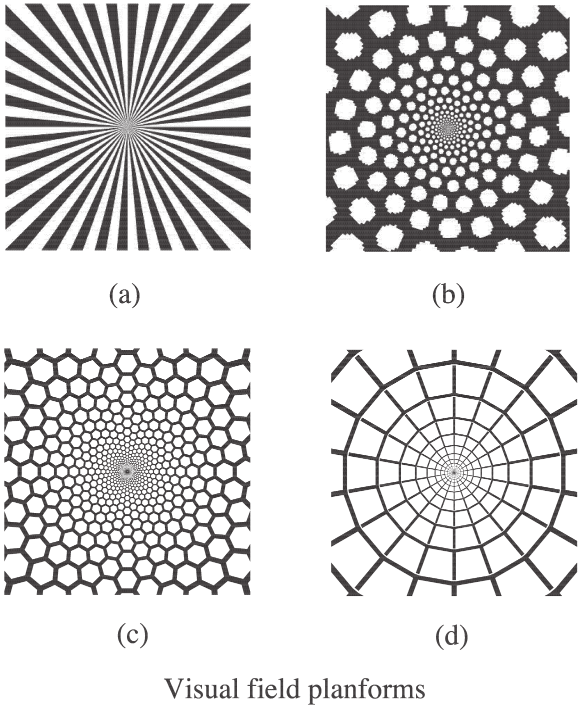
Figure 10: Short and long range connections in the visual cortex. · · · inhibitory; · – · – · – excitatory.

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.


(a) (b)

(c) (d)

Visual field planforms

Figure 11: Taken from Bressloff et al. 2002

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Prof. Dr. Martin Golubitsky
The Ohio State University
Mathematical Biosciences Institute
Columbus, OH 43215
USA
mg@mbi.osu.edu