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Behavioral Variability in the Service of Constancy

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From a stimulus-response (S-R) point of view, or even with an intermediate step, involving cognition (S-O-R), the existence of behavioral variablity in organisms, even under tightly controlled experimental conditions, suggests that 1) the relevant inputs to the system have not been fully characterized, 2) even the most minute difference in system inputs can produce vastly variable behavioral output, or 3) that behavior is fundamentally variable. Any of these possibilities leads to the conclusion that precise behavioral prediction, at any given moment, is virtually impossible. One can, however, re-conceptualize the challenge of understanding behavior such that it involves not what the organism will do from moment to moment, but what the characteristics of the system that governs the behavior of the organism are. In this paper, I outline a closed-loop cybernetic approach to understanding behavior, for which behavioral variability is actually a requirement. Findings are presented from a series of experiments across species, and using computer simulations, that support a cybernetic interpretation of behavior. I argue that behavioral variability provides adaptive advantages to organisms – regardless of whether that variability is produced by noise, or is actively generated by nervous systems. Finally, I discuss some ideas from embodied cognition that impose constraints on the variability of behavior.

The vast majority of ethological, psychological, and neuroscience (EPN) research, grounded in Behaviorist and Cognitive Theory, assumes that behavior is fundamentally stimulus-response (S-R) – that is, a behavioral *response* is the result of exposure to a stimulus or set of stimuli, either external or internal. In the modern instantiations of these theories, specific behaviors are thought to be learned by an organism as a means of controlling its environment (e.g., Rescorla, 1988). For example, a rat learns, through an understanding of the consequences of its actions, to press a bar because it understands that the outcome of this action is rewarding, in that it obtains a food pellet. Although the details of how responses are elicited vary in this example, depending on the specific theory used to explain it (e.g., Dickinson & Balleine, 2000; Sutton & Barto; 1998), these theories all contain the same underlying assumption that there is a linear and unidirectional relationship between stimulus *input* and behavioral *output* – even if it is the consequence of the behavioral output, not the behavior itself, that is important to the organism. If this is true, then if the conditions under which a rat learns to press a bar are exactly the same, it should always press the bar using the same behavior – that is, its behavior should be completely predictable. However, even in tightly-controlled experiments, the behavior of organisms is variable (Breland & Breland, 1961; Neuringer, 2004). And in fact, it may be the case the behavior is actually fundamentally variable (Blough, 1966; Korobkova, Emonet, Vilar, Shimizu & Cluzel, 2004; Neuringer, 2002; 2004; Park, Pontius, Guet, Emonet & Cluzel, 2010). If behavioral variablity is fundamental, one would expect to observe what we do – broadly similar behavioral patterns, with behavioral variability playing little role, except as noise (however, see Brembs, 2011). However, models like those described above typically account for less than 40% of the observed variance in behavior (and often much less) (e.g., Armitage & Conner, 2001).

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There is, however, an alternative to the above view, based on the ideas of cybernetics (Rosenblueth, Wiener, & Bigelow, 1943; Rosenblueth & Wiener, 1945; Wiener, 1948). If we re-conceptualize behavior in different terms, behavioral variability takes on a more central role – becoming a necessary component of behavior, instead of unexplained noise. Rather than an organism controlling the outcome of an event by learning a specific behavior through its consequences (reward, negative reinforcement, or punishment), instead what the organism might be doing is varying its behavior in real time in order to control the levels of relevant variables. In the case where food is used as a reinforcer for a bar press, bar pressing itself becomes more likely, because bar pressing – however that is actually accomplished – ultimately reduces hunger. Hunger level, not the abstract concept of reward, is what is being controlled by the animal. And in order to control hunger, the organism must first learn to control other environmental variables that are related to the control of hunger, such as the orientation of its body with respect to the bar. Unlike the control of a behavioral outcome, control in this sense is an ongoing, dynamic process. Variable behavior is required for organisms because, unlike the environment inside an operant chamber, the real world, in which organisms evolved to navigate, is not static. Any number of minor to major disturbances, that are often unpredictable, can prevent an organism from, for instance, controlling its hunger level – or any of the perceptual variables related to hunger. Variability provides a means of compensating for these disturbances. This may seem like a minor and obtuse re-interpretation of the bar-pressing phenomenon, but it has major implications for the understanding of behavior. And crucially, models of this sort can account for as much as 99% of the variance observed in behavior (e.g., Marken, 1986, 1990).

In this paper, I will elaborate on a closed-loop, cybernetic theory of behavior, Perceptual Control Theory (PCT) (Powers, 1973), in addition to outlining some methodologies that can be used to investigate behavior using this model. In addition, I will argue that, in order for organisms to behave in flexible and adaptable ways, a degree of intrinsic variability is required. And although there seems to be a general lack of understanding of the mechanisms that create variability (e.g., Neuringer, 2004), I argue that this is not necessarily insurmountable obstacle to understanding behavior, if it is re-examined in the light of cybernetics.

Despite the fact that the formal field of cybernetics has existed for some time (Rosenblueth, Wiener & Bigelow, 1943; Rosenblueth & Wiener, 1945; Wiener, 1948), the ideas generated by it have largely failed to be adopted by researchers in EPN – even though much work in artificial intelligence and robotics assumes that the behavior of organisms that these systems are designed to emulate is cybernetic. I will argue that, not only does a cybernetic model provide a more powerful explanatory platform for understanding behavior than do linear models, but that variability is a crucial component of behavior. And, as opposed to linear models, that lead researchers to focus on what an animal is doing at a specific point in time in relation to a set of inputs, a cybernetic approach views behavior in terms of controlled variables – that is, the aspect(s) of the organism's internal or external environment that the behavior of the organism is produced in the service of changing or maintaining. In addition, although it is not antithetical to linear models of behavior, I will discuss the idea that behavior is often constrained by morphology, both of the organism, and of its environment, and that the rules that animals use to behave, cybernetic or not, are not abstract concepts encoded solely in the brain, but embedded in a larger system that includes the organism and its environment. This is an important consideration for a complete understanding of behavior.

So, What is the Problem?

Behavioral variability can refer to either within-organism variability in the same context, or between organism variability in the same context. Between-organism variability is generally seen as either genetic in nature or due to some early developmental experience – some fundamental preference – whereas within-organism variability is seen to be contextually dependent – the sum of the inputs to the organism at a particular time. Between-organism variability is well-known, and is the reason that within-subject designs tend to be more powerful – and one might suspect that small phenotypic variation could account for these individual differences. However, even in genetic clones reared in the same environments, observed behavior is highly variable (e.g., Sondergaard, Herskin, Ladewig, Holm & Dagnaes-Hansen, 2012). Within-organism variability presents an even greater problem in terms of explanation.

Although behavioral variability is well known in *higher* animals, such as mammals, this is, to some degree, seen as *acceptable*, given the complexity of their nervous systems, and corresponding opportunity for the introduction of noise and error. However, even the simplest of animals exhibit variability. For example, fruit flies, *Drosophila melanogaster,* are highly variable in their tendency to turn left or right in the optomotor task, and mathematical analysis suggests that this variability is not simply the result of noise (Maye, Hsieh, Sugihara & Brembs, 2007). Paramecia are known to switch direction spontaneously, even in homogeneous environments (Oosawa & Nakaoka, 1977). And even the lowly bacterium, *Escherichia coli*, exhibits what appears to be inherent behavioral variability that cannot be explained by appealing to the sum of its inputs (Korobkova et al., 2004; Park et al., 2010).

The Linear Model: A Very Brief History

In its infancy, Psychology strove to establish itself as a respectable science. Because the accepted model of experimental science at the time was derived from Newton's classical view of physics – that is, the sum of the external forces acting on an object fully explains the behavior of that object – Psychology adopted this approach to understanding the behavior of organisms as well. The linear model was embraced, despite the fact that early researchers, such as Wundt and James, recognized the role of purposefulness, and thus, an ability to be not only influenced by, but also to influence the environment, in the behavior of living things (Cziko, 2000).

Gradually, it became clear that some of the early psychological methodologies, such as the use of introspection, lacked the strict objectivity of proper scientific methods. Beginning with Pavlov, whose ideas were further developed by Watson and Skinner, a new paradigm in Psychology emerged – one that emphasized understanding the inputs into the system (the stimuli to which the organism was exposed) in relation to the resulting output (the behavioral response of the organism). Behaviorism saw several successes, with the characterization of behavioral phenomena in classical and operant-conditioning terms. However, despite the utility of these descriptions, they remain largely descriptors, rather than explanations of behavior. An animal is more likely to press a bar if, following that action previously, a reward is obtained. Operant theory, however, fails to explain why an animal should learn to press a bar, not only with the specific movement that had been rewarded (e.g., with the right paw) but also using completely different movements (e.g., pressure with the other paw, its nose, its hind end, etc...) (e.g., Breland & Breland, 1961; Neuringer, 2002). If it were the case that it was a specific action (a behavior) that was being reinforced, then doing something other than that action should not occur. Behaviorism, like most modern EPN theories, assumes that *behaviors* are tangible, discrete entities. Although Behaviorism offered some clear advantages over earlier methodologies in terms of standardization of experiments, replication, control, and objectivity, in addition to its assumption of the existence of parsable behaviors, it still relied on Newton's linear causality model.

Eventually, in the course of the Behaviorist program, it became evident that not every animal could be reliably trained to perform any task, and that even under highly controlled conditions, behavior was variable (Breland & Breland, 1961). This violated the behaviorist assumption that the behavior of organisms is simply sums of their inputs. It was recognized that, at the very least, phylogeny is also a determining force in the production of behavior.

In attempts to address these issues and others, and in conjunction with ideas emerging from the development of the computer, the cognitive revolution was born. Unlike Behaviorism, cognitive approaches asked questions about the mechanisms of how input was processed by the machinery of the brain to create output. Effectively, Cognitive theory adds one additional element to the Behaviorist S-R model: an intermediate processing step, S-O-R, where the O stands for the organism (Hebb, 1949). Although many cognitive theories include various sorts of feedback mechanisms within the processing aspect, they are still fundamentally linear theories. Similarly, early ethological theories posited complex internal mechanisms (e.g., the 'innate releasing mechanism'), and so had more in common with modern cognitive approaches than they did with contemporary Behaviorist theories. Nonetheless, like Behaviorism and Cognitivism, in ethology the animal's behavior is in large part dependent on the incoming input, as particular 'fixed action patterns' (phylogenetically shaped motor outputs) are released by appropriate 'sign stimuli' (Lorenz, 1981). That is, ethological, behaviorist and cognitive theories, which underpin the majority of current EPN research, all ignore the fact that, not only does the environment act on organisms, but that organisms *also* act on the environment.

Cybernetics: An Alternative to S-R

The problem of behavioral prediction in a proximate sense – that is, what the organism will do, specifically, from moment to moment – is difficult to resolve, in light of behavioral variability. Will a cat bat you with her paw, or meow loudly in your ear to get your attention? What if this is not the important question, or at least not the whole question? What if we ask, instead, what the goal of the organism is – what are the important variables that the organism might be trying to control with its behavior?

The field of cybernetics, derived from developments in physiology and control systems engineering, asserts that that many types of behavior in organisms is teleological and goal-directed. The most relevant cybernetically-based theory for EPN research is PCT (Cziko, 2000; Marken & Mansell, 2013; Powers, 1973; Yin, 2013), which builds primarily upon the work of Ashby (1956). The basic tenet of PCT is that *goal states* are achieved by organisms through the implementation of negative feedback control mechanisms, the principle mechanism governing homeostatic systems. These mechanisms monitor the disparity (error) between the *ideal* (goal) values of salient perceptual variables, and the actual perceived values of those variables, producing variable behavior as a method of minimizing that error. In other words, the behavior of the organism is a means of controlling the values of important variables. The control systems can be hierarchically arranged, such that higher-order organizational mechanisms take as their input the output from lower-order sensory control mechanisms (Vancouver, 2005). A goal does not necessarily imply conscious purposefulness on the part of an organism. Any homeostatic system has a *preferred* (goal) state, which is the set point of the parameter of interest for that system. The system does not need to *know* what the goal state is.

A classic example of a non-biological control system is a household thermostat. Its goal is to maintain a particular temperature that has been set by the operator. If the temperature that the thermostat measures is lower than the goal temperature, it activates the furnace. The activation of the furnace changes the temperature in the room, and hence the input to the thermostat, until the goal temperature is reached, at which point, the furnace is shut off. The behavior of the thermostat itself affects its subsequent behavior via negative feedback. Importantly, the thermostat does not know what the goal temperature is. And this type of thermostat has only two behavioral states – furnace on, or furnace off.

One could view the turning on and shutting off of the furnace by the thermostat as independent S-R events, noting that the furnace was turned on when the temperature was too low, and that it was shut off when the ambient temperature of the room matched or exceeded the temperature set by the operator. But what was that actual *cause* of, in particular, the shutting off of the furnace at the matched temperature? In fact, it was the previous behavior of the thermostat (turning on the furnace) that caused its own later behavior (shutting off the furnace). Part of the input to the system was the system's own behavior. Artificially parsing the behaviors of the thermostat into temporally disparate events causes the observer to miss the fundamental dynamics of the behavior of the system as a whole – that is, that the two events are not unrelated, and in fact, are intrinsically and continuously interconnected.

Several of the founders of cybernetics speculated, in one of the earliest papers on the subject, that many behaviors observed in organisms would turn out to be of the type found in artificial control structures such as thermostats (Rosenblueth, Wiener, & Bigelow, 1943), and Ashby (1952) recognized that the control of at least some variables in organisms, which he called *essential variables* – things like hunger level -- should be selected for by evolution. In later work, methods were outlined with which the control system properties of organisms could be tested using robotics (Rosenblueth & Wiener, 1945). Since that time, cybernetic theory has been applied to robotics and artificial intelligence (e.g., Johnston, 2008; Nahodil & Vitku, 2012), has been fairly extensively used in sociology (see Robinson, 2007) and economics (e.g., Cochrane & Graham, 1976), and has even been applied to clinical psychology (Carey, 2006). However, researchers seem to have generally skipped the investigation of the actual behavior of the organisms in favor of moving straight to application – where it has often proved useful. Because of this, it is all the more puzzling that EPN has remained more or less firmly entrenched in linear ideology (Marken & Mansell, 2013).

Others have proposed theories that have employed various types of feedforward and feedback in their architecture, such as Reinforcement Learning (Sutton & Barto, 1998), and the Associative Cybernetic Model (Dickinson & Balleine, 2000), as well as the work of Tolman (1932, 1948). On the surface, these seem compatible with PCT; however, there is one major difference. In these models, feedforward and feedback mechanisms are used to refine the acquisition of a specific behavior, generally by modifying the organism's prediction of the consequences of this behavior. That is, feedback is not used to continuously modify the production of behavior itself, but rather to change the probability that a *specific* behavior will recur, given a set of inputs. Behavior is therefore discontinuous, and any artificial embodiment of these theories requires that, at some point, there is a distinct *switch* between behaviors – that is, artificial models based on these theories are necessarily finite state machines.

Rescorla (1988) has noted that modern behavioral theory explains behavior as the method used by the organism to control its environment, by correcting the misalignment between a goal (consequence of behavior) and its present reality. This requires not only that an organism understand the consequences of its actions, but often that it have an internal representation of at least a rudimentary version of its ideal state. It is no wonder that many make a distinction between *automatic* S-R tasks and true goal-directed behavior, attributing the latter only to more sophisticated organisms – and then, only in some situations (e.g., Dickinson & Balleine, 2000).

In contrast, a control system does not require an internal representation of the consequences of its actions, nor is there a true distinction between automatic and goal-directed behavior. All behavior is seen to be goal-directed, according to PCT, as it is performed in the service of controlling relevant variables. Control systems do not require complex internal representations because they monitor only the level of a perceptual variable and contrast that against the ideal level, producing variable behavior if the error is too high. But, since the error signal from lower-order control structures can be fed into higher-order structures, one can imagine that, given a complex enough system of control structures controlling a large enough number of variables, behavior might appear *as though* the organism has an internal representation of the world and of the consequences of its actions. In addition, because online error correction with respect to controlled variables is the focus, rather than the production of specific behaviors, the transition between observable behaviors can be much more graded. These basic ideas are demonstrated in a non-learning context in the simulation section of this paper (below).

In a learning context, modern behavioral theories (e.g., Dickinson & Balleine, 2000; Rescorla & Wager, 1972; Sutton & Barto, 1998) describe the content of learning in terms of the acquisition of specific behaviors that minimize the disparity between the organism's internal representation of its ideal state and its actual state, with respect to various stimulus inputs, including the entity's own estimation of the consequences of its actions (short and long-term). Alternately, PCT describes learning as the process of altering the parameters of control systems that underlie behavior, which is termed *re-organization*, in the face of changing environmental conditions. In situations where there is little environmental disturbance and the conditions are often the same, high-level re-organization does not need to occur, and compensation need only take place at very low, sensory levels, so the behavior appears to be automatic or stereotyped. Although a full treatment of learning is outside the scope of this paper, it is described in detail, including some potential neurophysiological underpinnings, by Yin (2013). Importantly, the principle of re-organization has been demonstrated by the creation of both simulated and robotic systems using hierarchically-arranged control structures that learn by randomly shifting control system parameters (e.g., Powers, 2008; Young, 2000). The resulting acquired behavioral patterns observed in the simulated entities are broadly similar in their execution over time, but exhibit the kinds of behavioral variability seen in real organisms, and crucially, are adaptable in the face of the introduction of various types of disturbances. This learning occurs, despite the fact that the simulated organisms lack an internal representation of any sort, other than the preferred value for the specific parameter with which they are concerned.

Although the theory and philosophy of cybernetics has been fairly well developed, even for the application to EPN (e.g., Ashby, 1956; Cziko, 2000; Powers, 1973; Wiener, 1948), and its usefulness for the construction of artificial systems has been established, the basic premise that organisms themselves behave like control systems as opposed to S-R systems has remained, by and large, empirically untested.

Are Organisms Cybernetic? Some Clues From Behavior

Although the majority of EPN research describes organisms as linear machines, there is evidence in the literature that many organisms function like control systems. For example, to catch thrown objects, both dogs and humans maintain constant the linear optical trajectory – that is, the angle of the object on the retina with respect to the horizon (McBeath, Schaffer, & Kaiser, 1995; Schaffer & McBeath, 2002; Schaffer, Krauchunas, Eddly, & McBeath, 2004). Predatory flatworms track prey by maintaining constant the perception of mucus trails (Iwai, Sugiura & Chiba, 2010). Male crickets performing the ‘judder’, the back and forth movement performed in agonistic interactions, keep their bodies horizontal to the substrate, regardless of the incline of the substrate, by varying the specific movements used (Pellis, Gray, & Cade, 2009). Jellyfish appear to have a number of internal reference values for perceptual variables that they control with their behaviour using feedback systems: salinity levels, turbulence, somatosensory stimulation, the formation of aggregations, and direction of swimming (Albert, 2011). Spontaneous magnetic alignment in many types of organisms suggests that geomagnetic direction is a controlled variable (e.g., Begall, Cerveny, Neef, Vojtech, & Burda, 2008; Nogueira & Lins de Barros, 1995; Rothsey & Rohde, 2002; Vácha, Kvíčalová, & Pužová , 2009). The carrion beetle, *Necrophorus humator*, maintains constant a certain wind direction with respect to the direction in which it is travelling (Böhm, Heinzel, Scharstein, & Wendler, 1991). In birds, although the specific movements used to accomplish flight vary widely, the aerodynamic forces involved are controlled in a consistent direction with respect to gravity (Dial, Jackson, & Segre, 2008). Complex social interactions in mammals and birds have also been shown to involve the homeostatic maintenance of inter-animal distance and/or inter-animal bodily orientations (e.g., Golani, 1976; Moran, Fentress, & Golani, 1981; Pellis, 1982). In all these cases, the animals vary their behavior in order to keep constant some perception (Powers, 1973).

Are Organisms Cybernetic? Some Research Methodology

Dodging Rats

As opposed to the examples given above, the vast majority of behavioral descriptions in the literature are formulated in linear terms – the manipulation of one or more input variable(s) changes the resulting behavior in some way. Because of this, the focus of my research has been to test, explicitly, whether or not some behaviors, previously thought of as linear systems, can be re-defined in terms of, and better understood as arising from, cybernetic mechanisms. At the outset, it was decided to investigate a behavior that had previously been described as an S-R system, robbing and dodging in rats. Robbing and dodging is a food-protective behavior, whereby one rat, the *dodger*, who is in possession of a food item, pivots laterally away from a conspecific, the *robber*, in order to evade the attempts by the robber to steal its food. The dodger holds the food item in its forepaws, and the robber generally approaches the dodger from the front (Whishaw, 1988; Whishaw & Tomie, 1988; Whishaw, DuBois, & Field, 1998). Previous work had suggested that the magnitude of the two-dimensional angle swept out by the dodger (viewed from above or below) during the pivot was directly related to contextual information, such as the quality of food being consumed, as well as relative partner identity (i.e., dominant or subordinate) (Whishaw & Gorny, 1994; Pellis, Hastings, Shimizu, Kamitakahara, & Komorowska, 2006).

However, given that rats are able to learn, if relatively fixed dodging angles were being used by the dodger – once the dodge were initiated, the dodger would not change its behavior, regardless of the subsequent behavior of the robber – the robber would eventually learn this, and so it would seem reasonable that the robber would be able to defeat the dodger. In fact, robbers *rarely* defeat dodgers, implying that, either robbers are unable to learn, or that the description of the system was incorrect.

A simple way for the dodger to continuously solve the problem of the robber's food-stealing attempts would be to maintain a minimum distance between itself (specifically, the front of itself, where the food is located) and the *stealing end* (front) of the robber. This is a cybernetic rule, whereby the dodger, in real time, controls the distance between itself and the robber, compensating for the movements of the robber. It should be noted that the robber might also be using a cybernetic rule to rob – but instead of *maintaining* its distance to the food, its goal would be to *reduce* its distance to the food to zero.

In order to test the cybernetic hypothesis against the original S-R description of robbing and dodging, the variability in the magnitude of the dodging angle was compared to the variability in the inter-animal distance. If it were the case that dodgers were behaving in an S-R fashion, it would be expected that the dodging angle should remain relatively constant when contextual information remains the same, whereas the inter-animal distance should be more variable. If, on the other hand, what was important to the dodger was inter-animal distance, it would be expected that the distance between the animals should remain relatively constant, with the dodging angle being more variable. After digitally tracking the dodging behavior of seven focal animals, each paired with both a dominant and a subordinate partner, and each given two different types of food, it was found that, in any given context, the dodging angle (and, in fact, every other parameter that was measured) was much more variable than the inter-animal distance. This was true both across and within individual animals (see Table 1; H. C. Bell & Pellis, 2011).

The second part of the analysis was to determine whether or not inter-animal distance were truly a controlled parameter. If a system is cybernetic, and is actively working to control a particular parameter, then, as the system is perturbed – as the value of the controlled parameter is altered – the system should compensate in order to return the parameter to its preferred level. A consequence of this property is that the level of the parameter should be uncorrelated with disturbances to the system. In the case of the rats, the robber perturbs the value of the controlled parameter (distance) by attempting to get close enough to the dodger to steal its food, reducing the inter-animal distance to a level below the dodger's preferred minimum. Thus, if distance is being controlled by the dodger, one would expect that inter-animal distance should not be correlated with the movement of the robber – in this case, the angle swept out by the robber during its robbing attempt. The relationship between inter-animal distance and robber angle was compared, and no correlation was found (see Figure 1). However, in order to ensure that the system was operating the way it was thought to be, the movement of the robber was compared to that of the dodger – variables that should be correlated if the movement of the two animals are related to one-another, which should be the case if the animals compensate for each other's movements. There was, indeed, a significant correlation between robber and dodger angle (see Figure 1).

Table 1
Coefficients of variation, for each animal, of distance and dodger angle

Subject	Distance	Dodger angle
1	0.274	0.374
2	0.320	0.472
3	0.244	0.391
4	0.278	0.345
5	0.346	0.439
6	0.339	0.401
7	0.353	0.467
Mean	0.308	0.413

Note. From Bell & Pellis (2011).

Finally, it was found that, in fact, contextual information *did* influence dodging decisions – but not in the way previously described. The inter-animal distance at the onset of the dodge varied with respect to two types of contextual information, food type and partner identity. In our study, these two variables produced effects on initial distance mainly through difficult-to-interpret interactions. Additionally, the preferred minimum distance (the distance maintained by the dodger) varied as a function of partner identity, but not food type. Together, these findings suggest that some contextual information influences the parameters of the underlying control systems governing the behavior of the dodger. For example, in some situations, it might be prudent for the dodger to maintain a greater minimum distance, whereas in others, a smaller distance will suffice – that is, the preferred value of the controlled variable could itself be changed by contextual information. Alternatively, especially in the case of the modified initial distance, it may have been the case that the parameters of the effectors of the control system governing food protection had been altered – in this case, the speed at which the muscle fibers of the dodgers were engaged. It is important to note that observable behavior of a control system or set of control systems can be affected by changing any number of the parameters of its constituent components (see Powers, 1973), but because our purpose was not to answer that question specifically, the above experimental design did not allow us to address it directly.

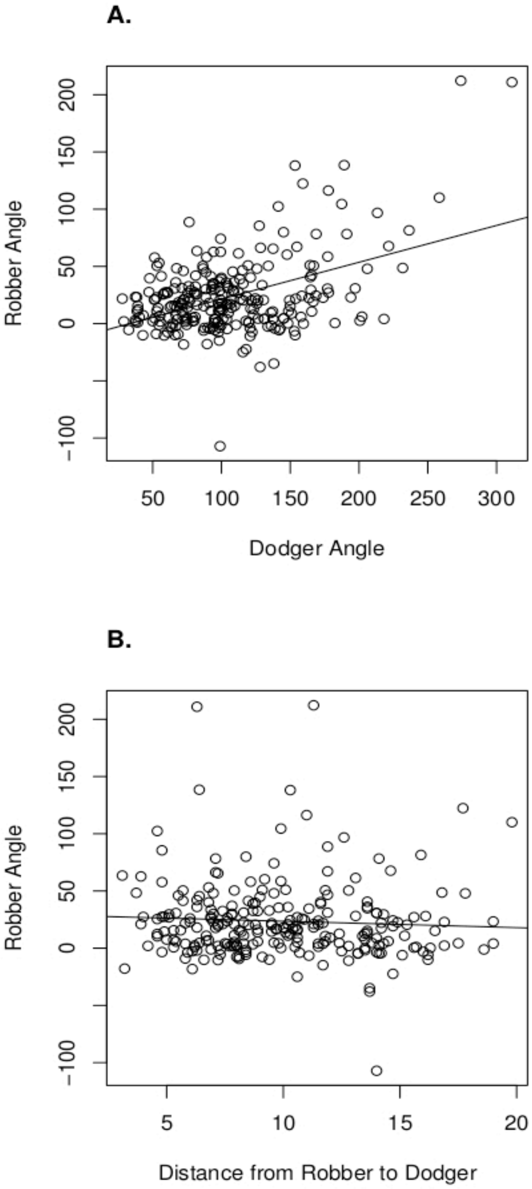


Figure 1. From Bell & Pellis (2011). Correlations between (A) robber angle and dodger angle, and (B) robber angle and interanimal distance.

How Widespread is the Cybernetic Dodging Rule?

If it is the case that rats use a cybernetic rule when protecting food, and given that food protection is a ubiquitous problem for organisms, one might ask if other species implement similar types of rules when engaging in similar behavior – and just how far away, in phylogenetic terms, might these types of rules continue to be found? Fortunately, I was made aware of another group of animals, separated from rats by about 500 million years of evolutionary history, that also use dodging to protect food: crickets.

Some have argued that crickets, and arthropods in general, have nervous systems so simple that they *must* be S-R machines, and that their behavior is essentially ballistic (W. Bell, 1991; Schöne, 1984). In other words, the nervous system of crickets lacks the necessary sophistication enabling the processing of information quickly enough to update behavior once it is initiated, resulting in the reliance on relatively stable sets of information, such as contextual cues, to behave. Again, the two competing hypotheses were pitted against one-another.

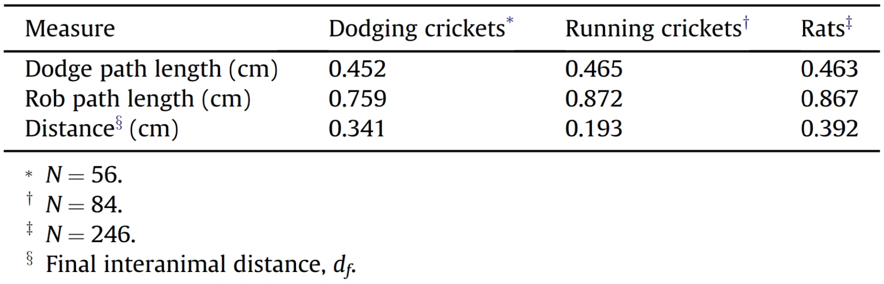
The analysis began by measuring variability in inter-animal distance *versus*, in the case of the crickets, the path length of the dodger. Path length was measured because, unlike rats, which use pivoting most of the time (and only the instances in which pivoting was performed were evaluated) to evade a robber, crickets are just as likely to run straight away from a robber as they are to pivot, depending on whether the robber approaches the dodger from the front or the rear. If the front is approached, the dodger pivots; however, the dodger will run straight away if approached from the rear. The crucial point is that, whether the dodge angle or path length is used, it is a proxy measure for the movement of the dodger, and should be relatively constant, if behavior is essentially ballistic. It should be noted that the rat data were re-analyzed using path lengths instead of angles, and that the results were unchanged. As was the case with the rats, inter-animal distance was significantly less variable than any other parameter measured (see Table 2), was not correlated with the movement of the robber, and the movement of the robber was correlated with the movement of the dodger (see Figure 2) (H. C. Bell, Judge, Johnson, Cade, & Pellis, 2012). It was concluded, therefore, that crickets use the same cybernetic distance regulation rule that rats use to protect food from conspecifics.

How Robust is This Cybernetic System?

In order to elucidate the properties of the cybernetic food defensive system further, the robustness of the system to disturbance was analyzed. This was done in two main ways: by disrupting the sensory inputs to the dodger, and by altering the way in which sensory input was processed by the brain of the dodger in rats. It was predicted that, given the importance of eating to survival, dodging should be fairly robust to minor disturbances, but that more major disruptions would alter at least some parameters of the system, or even drive the system to become S-R. It should be noted that the distinction is somewhat trivial, because a disrupted cybernetic system – for example, in the absence of enough sensory information for the organism to compensate for the actions of conspecifics (therefore appearing to be S-R) – can still be fundamentally cybernetic. There need not be any kind of switch to a different kind of rule or way of processing incoming information about the environment. The cybernetic rule would continue to exist, but the organism would be incapable of instantiating it, because it would be incapable of compensation. In fact, Rosenblueth, Wiener, and Bigelow (1943) speculated that some normal behaviors, such as a frog striking at a fly, are essentially S-R, because they occur so quickly that adjustments made based on feedback once the movements have been initiated are not possible. But even a striking behavior can, in some larger sense, be viewed as cybernetic – because the animal will surely try again if it misses (and the prey is still there).

Table 2

Coefficients of variation for dodging crickets, running crickets, and rats, of dodger and robber path length, and inter-animal distance



Measure	Dodging crickets[*]	Running crickets[†]	Rats[‡]
Dodge path length (cm)	0.452	0.465	0.463
Rob path length (cm)	0.759	0.872	0.867
Distance[§] (cm)	0.341	0.193	0.392

[*] $N = 56$.
[†] $N = 84$.
[‡] $N = 246$.
[§] Final interanimal distance, d_f.

Note. From Bell et al. (2012).

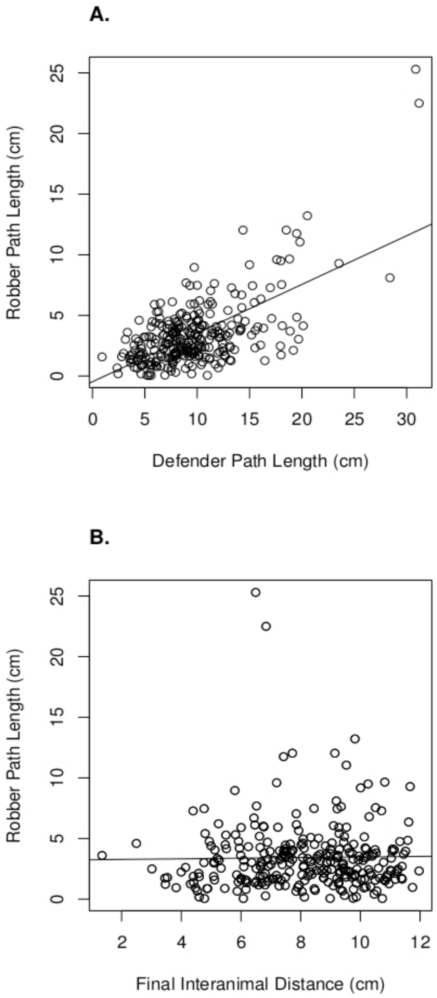


Figure 2. From Bell et al. (2012). (A) Correlation between robber path length and defender path length. (B) Correlation between robber path length and interanimal distance.

To begin with, the dodger's ability to use its tactile sense was impaired by shaving off its whiskers. This was done because it is known that rats use their whiskers to perform a variety of tasks (e.g., Bermejo, Harvey, Gao, & Zeigler, 1996; Carvell & Simons, 1995), and that removing the vibrissae modifies performance on those tasks. The results for the dodgers with shaved whiskers were not statistically different from intact controls, in that the same pattern of correlations was seen as had been observed in intact controls (H.C. Bell, 2014). Because the rats were behaving under lighted conditions, it is likely that their vision was sufficient to produce the behavior, even in the absence of some tactile input. The second experiment involved disrupting both the visual and tactile inputs of the dodger. Once again, inter-animal distance was controlled by the animals; however, the specific value of that parameter was altered, in that the maintained distance was smaller. This is not surprising, given that the range at which the dodger was able to detect the robber was diminished, as compared with intact animals. In effect, the preferred distance itself was likely not altered, but the ability of the dodger to detect the robber was instead compromised (Bell, 2014).

In the third experiment, control over sensory input was altered indirectly by changing the development of the brain during the juvenile period. It is known that raising rats in isolation changes several aspects of their behavior (Jones, Marsden, & Robbins, 2001), including some aspects of dodging behavior (Pellis, Field, & Whishaw, 1999). What seems to be the crucial experience lacking when rats are isolated during the juvenile period is that they are unable to engage in rough and tumble play with other juveniles. Rats raised with the ability to interact with – but not to play with – conspecifics produces many of the same deficits in social behavior as rats reared without any social contact at all (Pellis & Pellis, 2006). In addition, when the brains of rats raised in conditions without access to other juveniles are analysed, alterations are seen in the neuronal morphology in both the medial prefrontal and orbitofrontal cortices (H. C. Bell, Pellis, & Kolb, 2010).

When the behavior of dodgers that were raised in isolation was analysed, it was found that all aspects of the dodges remained the same as in the controls, *except* that the preferred minimum distance was increased (see Figure 3). In contrast to the sensory manipulations above that impaired the dodger's ability to detect the robber, it seems likely that, in this case, the internal reference value of the distance parameter was altered. Importantly, for this work, it can be seen that the rat continues to adhere to the cybernetic distance-regulation rule (H. C. Bell, 2014). The isolation-reared rats became hyper-sensitive to the approach of conspecifics, possibly because they lacked experience interacting with others that would allow for a more nuanced reaction. Interestingly, a similar effect on inter-animal distance regulation in rats while performing other behaviors seems to arise from domestication. During play fighting, the distance at which a defender begins to react to an attacker differs, with wild rats reacting at twice the distance of domesticated rats (Himmler, Stryjek, Modinska, Derkson, Pisula, & Pellis, 2013).

Can We Simulate the Behavior?

One way to test whether or not one has correctly understood the behavior of an animal is to simulate that behavior using the experimentally-derived rules, to see if the simulation behaves in the same way as the real organism (Schank & Alberts, 1997). I used MASON, a library written in Java (Luke, Cioffi-Revilla, Panait, Sullivan, & Balan, 2005), to create an agent-based model of the rat dodging system. The primary advantage of using an agent-based approach is that it allows the different agents in the simulation to be heterogeneous – that is, to possess different properties – as opposed to representative agent models, in which all agents of the same type are given identical properties. This is a key point, because the goal of the robber is to steal the food from the dodger; whereas the goal of the dodger is to evade the robbing attempt – that is, the goal of the two agents is not the same.

The dodger was given one rule: once it possessed a piece of food, it was to maintain a minimum distance between itself and the robber (i.e., if the robber were too close, it was programmed to simply *do something* until the robber was no longer too close). Specifically, the dodger monitored the distance between itself and the robber, and when this distance became too small, the dodger would implement a correlated random walk until the boundary condition was again satisfied. With respect to the robber, its only rule was to try to get as close to the food as possible, with the tracking of the food becoming proportionally better as it got closer. However, the robber's rule was modulated, as the robber was also instilled with a varying degree of *motivation* to track the food, whereby, after a few attempts to steal the food, it would move away from the dodger. With these two basic cybernetic rules, in conjunction with the constraints placed on movement by, for instance, not being allowed to overlap with the other agent, the dodging behavior seen in actual rats and crickets was reliably replicated. In this simulation, it was even seen that if the robber approached the front of the dodger, the dodger would pivot away, but that the dodger would move off in a straight line if approached from behind, which was the same behavior observed in the crickets (H. C. Bell, 2014). Most importantly, this was accomplished without an internal representation of the world, nor of a prediction about the consequences of behavior. In fact, the only thing that the dodger was *aware* of was the distance between itself and the robber. Further, the method by which the simulated robbers and dodgers measured distance (trigonometry) was presumably completely different from that used by the real animals. Thus, what was demonstrated here was that the cybernetic rule itself, not the particulars of how it is instantiated, is the important element governing behavior. In light of this finding, the fact that rats and crickets can use the same cybernetic distance-regulation rule becomes much less surprising.

What If You Do Not Know What is Being Controlled?

Unlike the case of the rats and crickets, there are many instances in which it is not necessarily obvious what, if any, variable is being controlled by the organism. Also, unlike dodging, there are many behaviors that are not obviously tracking behaviors. Could these other types of behavior be under cybernetic control? And if so, how can we narrow down the possible controlled variables in the system?

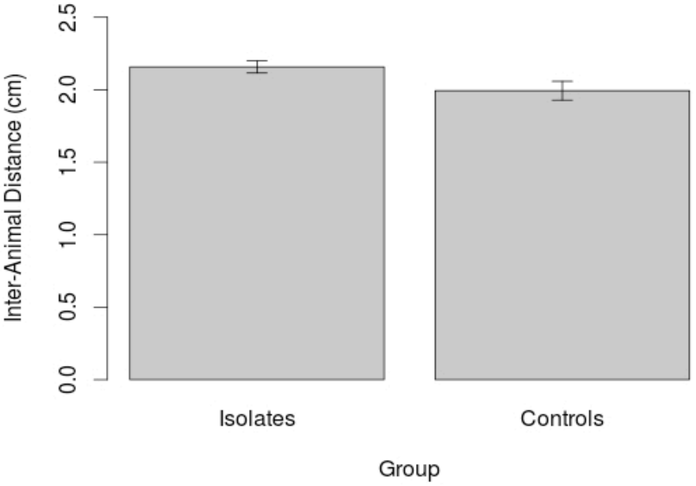


Figure 3. Inter-animal distance in isolates versus controls, $t(103.861) = 2.13$, $p < 0.05$.

One possible approach involves tracking the movements of animals with software, analyzing every possible parameter, and then determining which parameters from that list remain the most stable. Although this certainly could be an effective strategy, one could also imagine that this would be a rather arduous task, generating a lot of data, and it is certainly possible that the controlled parameter might be missed. An alternative approach is to use a technique that focuses the researcher's attention on features of the animal's behavior that are maintained constant relative to its partner. Such a technique is the Eshkol-Wachman Movement Notation (EWMN) (e.g., Golani, 1976; Pellis, 2011).

EWMN enables the experimenter to track the movements of parts of organisms, and of organisms as a whole, in relation to their other parts, to other organisms, and to aspects of the environment (Eshkol & Wachman, 1958). The resulting score, not unlike musical notation, is comprised of specialized symbols, which allows a trained reader to re-create the animals' movements without having seen the behaving animals. By juxtaposing the animals' movements in different frames of reference, with respect to their own body movements, to those of their partner and to the environment, one can identify constancies in the behavior of the animals (e.g., Golani, 1976; Moran, Fentress, & Golani, 1981; Pellis, 1982).

For example, in the combat of male sage-grouse (*Centrocercus urophasianus*) the birds approach one another face-to-face, then stand shoulder-to-shoulder and maintain this orientation. From this position, the birds attempt to hit each other on the head with wing strikes (Wiley, 1973). An EWMN analysis showed that this shoulder-to-shoulder also afforded the birds the opportunity to defend against these wing strikes, and so the birds maintained the optimal orientation to avoid being hit, while simultaneously positioning themselves to launch an attack. This combined attack and defense maneuvering involved one bird performing compensatory movements to block the other bird from gaining the most advantageous position from which to strike (Pellis, Blundell, Bell, Pellis, Krakauer, & Patricelli, 2013). The EWMN analysis uncovered the fact that the birds actively maintained their inter-animal orientation, despite both birds moving backwards, forwards, sideways, and in circles. Once candidates for constancies have been identified, other methodologies can be employed to test whether or not they actually exist.

In order to test such an approach, the combat behavior of male Madagascan hissing cockroaches, *Gramphadorhina portentosa,* was examined. Other researchers have previously described combat behavior in cockroaches as consisting of a suite of distinct behaviors (e.g., Clark, Beshear, & Moore, 1995; Clark & Moore, 1994). Given that during combat, the cockroaches often flip each other over onto their backs, it was postulated that the *distinct* behaviors observed may not actually be distinct, but rather, arise as a by-product of both animals simultaneously trying to flip one another over. A pilot study suggested that some behaviors observed during combat are by-products of a cybernetic rule that is being used simultaneously by both animals.

Clips of cockroach combat were described and analyzed using EWMN. The results of the analysis suggested that what each animal is attempting to do is to contact the flank area of the other animal, as this was the area that attackers were most often oriented toward when beginning an attack. This possibility was tested by schematically dividing the cockroach's body into four areas (see Figure 4), and then noting where strikes by an attacking animal were most likely to occur. It was hypothesized that the reason the animals were targeting the flanks, if this were indeed the case, was because it was the area on the body that is most likely to result in a flip when butted by an attacker. Therefore, in addition to noting where attackers contacted defenders, whether or not the contact resulted in a flip was also recorded. The analysis showed that, not only was the flank area the preferred target for contact (see Figure 5), it was also the area that, when contacted by an attacker, resulted in the highest proportion of flips (see Figure 6) (Long, Bell, Logue, Mishra, Cade, & Pellis, 2012). In terms of cybernetics, the cockroaches are not controlling a parameter in the same way as the rats and crickets were during robbing and dodging. Instead, their compensatory behavior is directed towards maintaining a particular orientation with respect to the other animal, in addition to minimizing the distance to the target.

The examples of combat in Madagascar hissing cockroaches and sage grouse demonstrate how EWMN can provide insight into what the animals are maintaining as constancies during interactions and so provide clues as to what variables may be under cybernetic control. Juxtaposing the movements of the two animals and the inter-animal relationship on an EWMN notated page provides a means by which such constancies can be identified (see Pellis et al., 2013), making the arduous task of seeking what animals are controlling much simpler.

Can Realistic Neural Hardware Act Like a Control System? The Role of Neuromorphic Engineering

As has been previously mentioned, cybernetic theory has been used successfully in both artificial intelligence and robotics. These applications provide some support for the idea that organisms use similar types of algorithms to produce behavior; however, the hardware on which they operate, in addition to the specific types of algorithms employed, tend to be biologically unrealisitic – in particular, with respect to the lack of parallel, asynchronous, analog processing. At some point, it must be demonstrated that biological systems, given their particular set of hardware and its corresponding constraints, are capable of acting as control systems in the behavioral domain. Using a neuromorphic engineering approach to modeling the behavior of organisms seems to be one potential means of more closely connecting the *wet* fields of EPN with AI and robotics with respect to cybernetics.

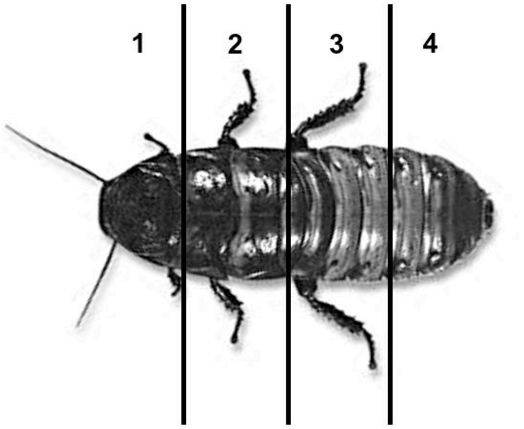


Figure 4. Four divisions of the cockroach body.

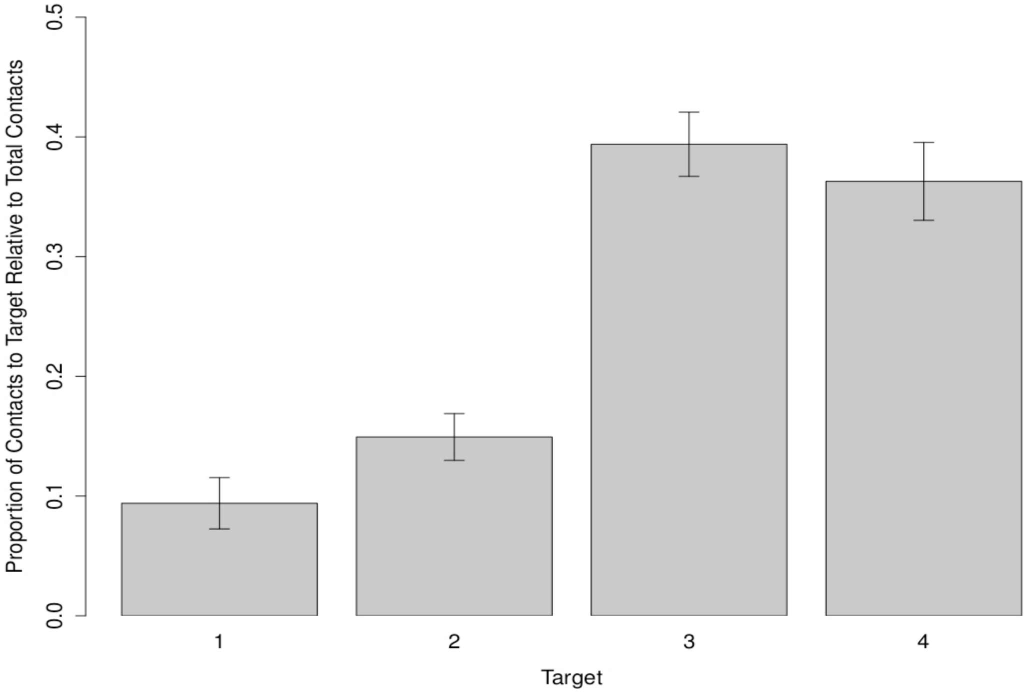


Figure 5. From Long et al. (2012) Proportion of contacts to each quarter: $F(3,69) = 25.90$, $p < 0.05$.

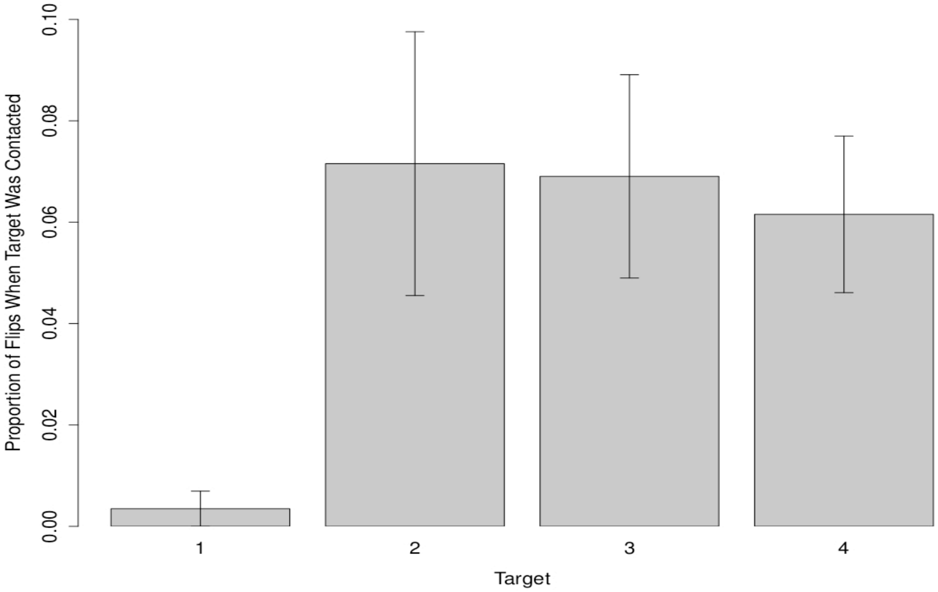


Figure 6. From Long et al. (2012) Proportion of flips relative to contacts on each quarter: $F(3,69) = 3.36$, $p < 0.05$.

Neuromorphic engineering, pioneered by Carver Mead, originally focused on the implementation of large scale analog, as opposed to digital, circuitry in the development of robotics and AI (Mead, 1990). The notion was that, because biological systems are far better at information processing than artificial systems, perhaps mimicking their function, which is analog, would lead to significant advances in AI. Since its inception, neuromorphic engineering has gradually come to be associated with broader aims of biomimicry, incorporating ideas from embodied cognition such that realistic neural hardware can be embedded in biologically plausible morphologies, which then act in the real world (e.g., Bernardet, Bermudez, & Verschure, 2012; Yang, Cameron, Lewinger, Webb, & Alan, 2012).

Ideally, a neuromorphic engineering approach could be used to demonstrate that the control system properties of organisms can actually be instantiated in artificial models with as close to the same properties as biological systems as possible, and there are several reasons why simply simulating behavior using methods such as agent based modeling are not fully satisfactory. These include the fact that robots do not require physical forces in the environment to be simulated, important aspects of which can be missed when creating virtual environments (Tamburrini & Datteri, 2005). By being required to act in the real world, insights are gained into how physical forces and the structure of the environment interact with the robotic agent to produce behavior. For example, even in as abstract a situation as the Prisoner's Dilemma, robotic agents were able to offer more insight into this behavior than were simulated agents (Grimaldi, 2012).

Given at least some branches of the current neuromorphic research program, arguments could certainly be made that this has already been done for some systems (e.g., Bernardet, Bermudez, & Verschure, 2012; Webb, 2008), but again, the question of why these insights have largely been ignored in the biological arena arises. And as with any modeling approach, there is always a risk that, even though the behavior of an organism can be reliably re-created, the details of the mechanisms of the model are incorrect (Webb, 2000). However, if a cybernetic rule can be enacted in an entity with both realistic body morphology, as well as neuronal hardware, it does at least suggest that the particular mechanism is plausible as an explanation for the behavior.

Mechanisms of Variability

At some level, it is not very helpful to state simply that variable behavior is produced in the service of achieving some goal state. Then the question becomes, regardless of what the goal of the animal is, how is variable behavior created to begin with? But do we really need to know this in order to understand behavior?

Ashby (1956) described his Law of Requisite Variety such that the larger the number of possible behavioral states of a control system, the larger the number of disturbances for which the system can compensate. In the case of the thermostat, there is only one possible disturbance to the system, which is when that the temperature is too high; therefore, the control system does not need to exhibit much variability in order to compensate. In contrast to the thermostat system, most organisms have multi-modal sensory equipment, which can detect graded differences in stimuli (analog), unlike the thermostat, which is binary – both in its sensory capacity, as well as its behavioral options. Additionally, most living organisms are subject to disturbances to relevant variables that are orders of magnitude greater in number, in addition to the number of variables themselves being much greater. It is therefore a necessary that a wide variety of control system behavior be available in order for the organism to compensate. And it is known that organisms are capable of implementing highly variable strategies in order to control relevant parameters (Golani, 1976; Pellis & Bell, 2011).

The observed behavioral variability may simply be the result of the exact state of the system at that moment, which is different from the state of the system at previous time points, even under the same external conditions (i.e., slightly different initial network states, including the embedded nature of the neural hardware in the rest of the system, any parameter of which, when varying slightly, can lead to vastly different final states), or it may be the case that behavioral variability is a fundamental component of the system -- and perhaps extreme sensitivity to initial conditions of the system produces variability that is, for all practical purposes, irreducible. Further, it is possible that organisms somehow co-opt and amplify environmental variability (e.g., quantum effects) in order to produce variable behavior. These possible mechanisms are not necessarily mutually exclusive. Regardless, the ability of biological networks to generate spontaneous activity has been well documented (e.g., Mazzoni, Broccard, Garcia-Perez, Bonifazi, Ruaro, & Torre, 2007). Variability, therefore, need not be directly selected for, although it may be adaptive, and may simply arise because of the chaotic properties of the behavior of networks, which seems to occur in even very small systems (e.g., Sabarathinam et al., 2013).

However, it seems likely that fundamentally variable behavior should be important for organisms, in that it decreases, for example, the ability of other potential predator (or prey) organisms of learning to predict the behavior of the focal organism accurately. For example, many prey animals have protean movements in their escape behavior, making it difficult for predators to keep tracking them (Driver & Humphries, 1988). There is some evidence to suggest that variability is actively generated by nervous systems, rather than being a by-product (Beck, Ma, Pitkow, Latham, & Pouget, 2012; Brembs, 2011). The fact that variable behavior can be reinforced in numerous species further supports the idea that variability is not simply the result of noisy inputs (Neuringer, 2004). Some argue that variability is necessary in order for the organism to learn about its environment effectively, called *world learning*. The reasoning is that variability, at least partially, allows the organism to *test* its environment (Brembs, 2011).

In fact, when the behavior of organisms is simulated, it seems to be the case that an element of randomness (i.e., variable behavior) needs to be included so that the agents do not, for instance, become trapped in corners (e.g., Powers, 2008). Even in *E. coli,* the movement of which is governed by the mechanical action of molecules, such as glucose, binding to receptors that activate its flagella, the bacterium will tumble randomly in the absence of bound molecules, which proves to be an effective strategy to locate a food source eventually (Koshland, 1980).

Constraints on Variability: The Embodiment of Cognition

Although behavior can be highly variable, there are also limits to how much variability is possible. Understanding the behavior of organisms also requires that one be aware, in addition to how neural processes produce behavior, the physical constraints on behavior – that is, that the shape of the organism, its biomechanics, how its nervous system is structured, and the physical characteristics of its environment, all ultimately contribute to observable behavior (Barrett, 2011). This is not a point of divide between linear and cybernetic theories of behavior; rather, it is simply another factor that is important for a complete understanding of behavior.

Early authors, such as Wentworth Thompson (1917), recognized the importance of physics as a driving force, as much as natural selection, in the development of the morphology of organisms. But it seems a much more recent development that the role of environmental and morphological constraints in shaping behavior have been investigated (e.g., Barrett, 2011; Pfeifer & Bongard, 2007). For example, the morphology of simulated agents has been demonstrated to affect their behavior so much that, for instance, differing numbers of body segments produce vastly different behavior, even though the algorithms governing behavior are the same (May, Schank, & Joshi, 2011). The degree of bilateral symmetry in artificial agents has also been shown to influence their locomotive efficiency in a virtual environment (Bongard & Paul, 2000). Even morphology of whiskers in both robots and simulated agents was demonstrated to alter the ability of robots and agents to follow walls in biologically realistic ways (Fend, Bovet, & Pfeifer, 2006). Thus, as was seen in the simulation experiment above, the role of the physics of the system must be taken into account when constructing a complete model of behavior.

Discussion

It is possible to view a cybernetic system in linear terms – that is, to *cut the loop* so that only an immediate input (or set of inputs) and output are considered. This approach, however, fails to capture the dynamic nature of the system, and the fact that the organism's own behavior alters the parameter(s) of the variable(s) being controlled, which affects its subsequent behavior. Crucially, it also makes the problem of behavioral variability both salient and intractable.

Cybernetic systems, if the behavior of organisms can truly be described in those terms, are not passive recipients of stimuli, but active participants in how stimuli are experienced. It is the difference between how a rock and a human behave when pushed. The rock can do nothing to counteract the applied force – that is, the behavior of a rock is truly a sum of the forces that act on it. In contrast, the human actively compensates to try to maintain an upright position. And in order to compensate, the behavior of the human, in terms of what muscle groups are activated when, is highly variable, depending on factors such as the topographical structure of the environment (is the ground he is standing on at an angle?), the speed with which he reacts (is he fully alert and anticipating this, or half asleep?), learning effects (has this happened before?), and genetic/epigenetic effects (how quickly and effectively is his brain and body able to process and compensate?), and perhaps an element of randomness – either intentionally or unintentionally generated by the interaction of all those parts – at any given moment.

Organisms are not inert objects, at the whims of the forces around them. They behave like machines that can act to alter both their internal and external environments – although some argue that even the machine metaphor is not general enough to capture the qualities of life entirely (e.g., Rosen, 1991).

Variability in behavior, even if the root causes of it remain unknown, does not render the behavior of organisms completely, or even largely, unintelligible – but it may be the case that precise, moment-to-moment behavioral prediction is not possible. By appealing to a closed-loop conception of organisms, the understanding of behavior can, instead, be approached on a different level. Instead of asking how a particular experimental manipulation alters the subsequent behavior of an organism, one might instead ask how an experimental manipulation alters the parameters of the system. This is a subtly different question, but the difference is important, and requires that the parameters of the system be understood to begin with. Understanding what variables organisms may be controlling necessitates that organisms be understood on their own terms *before* they are used as model systems to answer larger questions.

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