FLEXIBILITY AND CONSTRAINT IN BEHAVIORAL SYSTEMS

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Group Report: How Do Evolution and Behavior Interact?

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INTRODUCTION

Complexity in living organisms can arise very rapidly during evolution, and much of the history of life can be considered as a collection of "frozen accidents." Some of these occurred early, such as the universality of the genetic code, the machinery of protein synthesis, and excitable membranes; others occurred more recently, such as bilateral symmetry and cephalization. These events placed large constraints upon the avenues along which subsequent evolution could proceed. Because living organisms are, in a sense, encumbered with these contingencies, evolving organisms possess limited degrees of freedom for change and in many, but not all, instances can only "tinker" (Jacob 1977) with the existing framework. However, large degrees of behavioral diversity have proven possible, and dramatic changes, such as the origin of flight in insects, which had enormous consequences for the biosphere, were accomplished with relatively little change to the central nervous system (Edwards and Palka 1991). Our discussion of the evolution of behavioral diversity in the face of physiological and genetic constraints involved considering factors that contribute to phenotypic change at different levels of organization.

Behavior is *the* salient way to increase the flexibility of organisms and escape from these "frozen accidents" which constrain evolution. Behavior itself, however, is constrained at many levels of organization. First, it is restricted by the genotypic makeup of the organism. If genes subserve a number of behaviors (i.e., pleiotropy), then changes in one behavior are pitted against concomitant changes in a number of other behaviors or morphological structures. Thus, behavioral traits and morphological

traits are in some sense interlocked (via common gene circuits). If the genes associated with a particular behavior are completely fixed within a population, then of course there would be no evolutionary change possible other than by mutation. Another constraint imposed on behavior is the mode and structure of the sensory systems the organism possesses. An animal can only make use of those environmental stimuli it can detect. Finally, behavior is part of a hierarchy within and between living organisms that includes molecular, genetic, physiological, and social levels of interaction. The interactions between these levels can be complex, subtle, and bidirectional. This forces any study of behavior, at any of these levels, to consider the constraints imposed by other levels.

In this chapter we first consider the constraints on the evolution of behavior imposed by genetic factors. Next, we address the limitations imposed by the sensory system of an individual on behavior, and the evolution of behavior as well as the constraints imposed on the evolution of sensory systems by attendant environmental, physiological, and genetic factors. We also discuss the evolution of new sensory systems as well as the evolution of learned behavior and models of the evolution of learning. Finally, we explore the evolutionary consequences of the ability to learn.

CONSTRAINTS OF GENETIC PLEIOTROPY

Pleiotropy, or the multiple effects of a gene on the phenotype, places very large constraints not only on the behaviors of an organism, but on the molecular, morphological, and physiological organization of the organism as well. A powerful example of the constraints of genetic pleiotropy is the development of the body plan in animals. This involves gene clusters, homeobox genes (see Boncinelli, this volume) that are involved in the early establishment of the body plan and the blueprint and development of the nervous system (e.g., *Emx* and *Otx*). Homeobox genes of the *Hox* family have been conserved in evolution in a variety of metazoan groups; they control the cell identity of body regions along the anterior-posterior axis of the body. They probably arose as a cluster early in evolution, when the anterior-posterior axis was first established, and their organization and function proved to be a major constraint in the development of new body plans. Homeobox genes belonging to the *Emx* and *Otx* families are also conserved between flies and humans. Even if the main function of these genes is conserved, it is conceivable that they may perform additional tasks in different species, possibly through pathways of alternative splicing of mRNAs.

Although developmental processes often act as constraints on the further evolution of complexity in the structure and behavior of an organism, large changes may occur through a shift in the temporal and/or spatial expression pattern of key genes (e.g., *Hox* genes) that control parts of the body plan. These shifts in gene expression may have led to important reorganizations of the blueprint of the nervous system, offering new possibilities for brain functions and the generation of new behaviors. Thus, a slight displacement in the timing of gene expression could result in large changes in the

relative size and number of different brain regions (see Boncinelli, this volume), which in turn would give rise to significant changes in behavior.

Another example of pleiotropic genes that may constrain evolution are genes encoding enzymes involved in transmitter and neuropeptide production, proteins important for exocytosis, or proteins that function in signal transduction (Geraerts et al., this volume). Because of the various behaviors for which a single gene is responsible, selection of only one trait or process would be difficult to accomplish without producing changes, which may be maladaptive, in the other processes that the gene regulates.

The evolution of the pleiotropic gene necessarily affects all the processes that the gene regulates and, therefore, involves the evolution of functional integration. Flexibility in developmental expression of the gene (such as the small shifts discussed above) is a mechanism to escape constraints placed on evolution by the phenomenon of gene pleiotropy, and may lead to large changes in phenotypic organization. Alternatively, innovations are often accomplished by evolutionary mechanisms, such as gene duplication, which can be regarded as a relatively small change that would be less detrimental to the organism than mutating an existing gene. Here, one gene continues the old function, leaving the duplicate gene free to mutate and take up a novel function. Gene duplications offer other advantages as well. The related yet different proteins encoded by gene families may uniquely combine to regulate different but overlapping processes. In this way, with a relatively small number of genes, a disproportionately large number of processes and functions can be controlled. For example, combinatorial actions are shown by very different proteins serving as receptors, G proteins, and transcription factors. Similarly, modules consisting of families of proteins may be generated that can be recruited as a single entity during evolution to serve different functions (see Geraerts et al., this volume).

GENETIC SPECIFICITY

Like genetic pleiotropy with its accompanying constraints, genetic specificity (or the regulation of a particular behavior by a specific gene) has its own inherent constraints on the evolution of behavior. For instance, the gene encoding the egg-laying peptide prohormone of gastropod molluscs (such as *Aplysia* and *Lymnaea*) has been described in detail (Geraerts et al., this volume). This gene is expressed in a command peptidergic neuronal system that shows long-lasting electrical discharge activity during which the peptides are released into the circulation. The prohormone has a complex organization, and at least ten or eleven distinct peptides are transported in secretory granules towards the neurohemel endings and released in large amounts during prolonged periods of synchronous activity of the neurons making up the system.

Recent evidence (Geraerts et al., this volume) suggests that each peptide in *Lymnaea* is involved in the control of a distinct aspect of the egg-laying behavior. Egg

laying consists of a stereotyped series of overt behaviors involving a cessation of locomotion, turning of the caudal body, cleansing of the substrate surface (where the egg mass will be deposited), oviposition, and inspection, which are closely coordinated with reproductive physiology, i.e., ovulation and egg mass production. Some of the peptides that control these behaviors function in combination with another peptide of the same set. Furthermore, one peptide may fulfill various distinct functions associated with egg laying. Because peptides derived from one prohormone have multiple functions and act in coordination with other peptides (within the context of egg-laying behavior), there may be a constraint on the evolution of the encoding gene, and hence the behavior associated with this gene.

An alternative type of organization of a prohormone specific for behavior is found in insects, where the gene of interest encodes a simple prohormone from which only the eclosion hormone is derived (Truman, this volume). In contrast to molluscs, the eclosion hormone initiates all events of the complex sequence of eclosion behaviors.

CONSTRAINTS OF SENSORY SYSTEMS

Sensory systems are a critical interface between the organism and its environment. They impose constraints on the behavior of an organism and are themselves constrained by a number of factors within the environment and within the individual, including genetic and morphological factors. To understand the nature of the interaction between sensory systems and behavior, we need to address not only the constraints placed on sensory systems, but the mechanisms by which sensory systems constrain behavior.

There are often profound genetic constraints placed on evolving sensory systems that were imposed early in the evolution of life. For example, in *Drosophila melanogaster,* over two-thirds of the genome is used in optic lobe and eye construction (Thaker and Kankel 1992), so that major modifications to its eye are difficult to achieve. Adding novel proteins may allow some ommatidia to become ultraviolet sensitive; however, changes in the gross design of the eye cannot occur without affecting the entire organism. Thus, although genetic "tinkering" can occur to optimize the match between the sensory organ and the environment, the pleiotropic genetic interactions established early in evolution constrain (a) the changes that can be made to the eye and (b) the consequent behaviors that the visual system can ultimately generate.

Sensory systems are also constrained by the environment in which they occur. An example illustrating the complexity of the constraints on interactions between the sensory system of a behaving organism and its environment is that of vocal calling in male Tungara frogs (Ryan 1988). Males produce a mate call that is influenced by the sensory systems of the receivers in the following way. Females prefer males that produce complex calls over males that produce simple calls; females also prefer males

that produce lower frequency calls. In frogs, the fundamental frequency of sounds that can be produced by the larynx is a function of the mass of the vocal cords. Vocal cord mass, in turn, is allometrically related to overall body size (Ryan 1988). In addition, the sound frequencies that can be radiated efficiently by a frog are influenced by the size of the vocal sac relative to signal wavelengths. In response to female preference for lower frequency calls, male Tungara frogs have evolved a vocal apparatus that allows them to produce and transmit a call that is lower in fundamental frequency for their body size than is true for twenty-nine other species in the same subfamily (Leptodactylinae). This ability of Tungara frogs is accomplished by their having very large vocal sacs for their body size and perhaps by having relatively large vocal cords (Ryan 1988). Hence, the vocal apparatus of the male places constraints on its calling behavior. *Trachops cirrosus*, the bat that preys upon these frogs, identifies its prey by orienting preferentially to the complex frog calls. Although sexual selection for complex calls could possibly lead to evolutionary exaggeration of call structure, predators act as a constraint upon male signaling, and the degree of signal elaboration that occurs may be quite limited. Thus, the sensory apparatuses of the receiver and the production apparatus of the sender are intricately tied to each other as well as to the environment in which the calling behavior occurs. In another frog species, *Smilisca sila*, males produce more complex calls on moonlit nights, when they can see approaching bats and stop calling, and simpler calls on dark nights (Ryan 1988), when preying bats would be less visible.

Thus, male calling behavior is constrained by predation from bats, physical levels of light in the environment, the visual system of the caller, the preferences of the two species of receivers (frog and bat), the receivers' sensory apparatuses, and the vocal apparatus that produces the signal. Finally, ambient noise produced by conspecific and heterospecific animals, as well as by abiotic sources, also places constraints on male calling behavior. In the history of animal evolution, the fossil record indicates that predator/prey interactions must have been a continuing arms race, with predatory and evasive behavior pushing neural evolution to its limit (Roeder 1993).

THE EVOLUTION OF SENSORY SYSTEMS

Interactions at genetic, morphological, and environmental levels weave an intricate web of constraints around evolving sensory systems. However, despite these constraints, the diversity of sensory systems observed in different taxa is striking, suggesting that flexibility is an integral feature of sensory systems. Flexibility in existing sensory systems permits the organism to adjust its behavior in response to external cues from the environment, and the evolution of new sensory systems is a viable solution to the numerous internal and environmental constraints placed on the organism.

An important question is whether new sensory systems evolve from modifications to existing sensory systems, or whether they exploit an entirely new avenue of stimulus

detection and reception. The hair cells of the vertebrate octovalateralis system are thought to be an example of evolutionary modification of an existing sensory system (Jorgenson 1989; Will 1989). In this scenario, hair cells initially evolved in fish as part of a nonspecific lateral line alert system that responded to features of both water and sound waves. With subsequent vertebrate evolution, the lateral line system is seen as having differentiated into developmentally distinct subsystems, including electroreceptive organs in weakly electric fish, and vestibular and auditory organs in the inner ears of tetrapods.

The evolution of novel sensory systems has also occurred numerous times in evolution. For example, chordotonal (proprioceptive) organs have provided the source of tympanic auditory organs in several independent insect groups (Boyan 1993). Mantids have evolved a cyclopic ear as a detector of ultrasonic bat echolocation calls (Yager and Hoy 1987), and parasitoid tachinid flies have evolved a unique auditory organ for the detection of calls produced by cricket hosts (Heller 1992; Robert et al. 1992).

Whatever the means for evolving sensitivity to new stimuli, one can predict that sensory systems are adapted in their sensitivity to the entire set of relevant stimuli present in a species' environment. This prediction is supported by a number of observations. Lythgoe and Partridge (1989), for example, found good agreement between dichromatic pigment combinations in visual receptors and the visual stimuli associated with the discrimination of leaves and forest litter in forest-dwelling vertebrates, including grey squirrels, tree shrews, frogs, and dichromatic phenotypes of squirrel monkeys. In hymenopterans there is good congruence between the sensitivity spectra of three photoreceptor types found in compound eyes and the reflection spectra of angiosperm flowers on which these insects forage (Chittka and Menzel 1992).

Obvious constraints on the process of evolving new sensory systems are the medium through which the stimulus is transmitted and the dimensions of the physical world in which the organism will operate. More subtle constraints imposed on a newly evolving sensory system include the limitations of the sensory system from which it has evolved, and the constraints imposed by other sensory systems with which it will work in conjunction.

In communication systems where one organism produces a signal that is detected by another organism, there is a match between the structure of the signal and the tuning of the sensory receptor used by receivers to detect that signal. The mechanisms by which such coevolution of signal and receiver occurs remains controversial. It has been proposed that the same genes are involved in both production and recognition of sexual signals (Doherty and Hoy 1985). However, such close genetic coupling is not necessary for coevolution of a signal and receiver to occur (Butlin and Ritchie 1989; Boake 1991 and this volume). It may be productive to examine the variation within and between individuals when considering the evolution of signaling behavior because such variation might eventually lead to speciation in allopatric populations, as described in quantitative genetic models (Lande 1981; Lande and Kirkpatrick 1988).

LEARNED BEHAVIOR

We recognize that learned behaviors, as well as the ability to learn, can evolve (Thorpe 1963). However, the issue of selection of learned behavior is complex. In natural populations, behavior provides a means by which the organism is able to affect its niche as well as being passively affected by features in the environment. Conspecifics often share a common environment, and the behavior of one organism interacts with the behavior of other organisms. An act of one individual which influences the probability that another individual will act in a particular way may be termed communication. Learned behavior may allow communication between conspecifics to become more flexible than it is in species without learning. Like genetically determined communication, a requisite of learned communication is that a match exists between the sender and receiver. For instance, in the case of birdsong, which is a learned behavior, males show variation in the song learned and the ability to learn in general, while females have been shown to prefer the song produced by their species or by a particular dialect group within their species (see Brenowitz, this volume). Thus, this type of learned communication apparently involves a signal match and preference match between the sender and receiver respectively.

Because it is often difficult to evaluate directly the effects of learned behavior on the evolution of a species, computer-generated models of the evolution of learning, and of the evolutionary consequences of learning, can be a valuable tool to generate testable hypotheses. "Genetic algorithms" are simulations of the evolutionary changes affecting a single species and are based on models from population genetics (Goldberg 1989; Holland 1992). A population of individual genotypes is set up, initially at random. An ontogenic function mapping genotypes to phenotypes is applied to each individual, and a measure of their relative "fitness" is used to reproduce, differentially, offspring for the next generation. Changes (e.g., modeling mutation, sexual recombination) are made to some of these new genotypes, and the process begins again with this new population. Variations in selection, population structure, and ecological interactions have all been investigated in this fashion (Forrest 1993).

Neural networks are models of the changes to the individual due to learning, and are composed of a collection of interconnected neurons (Anderson and Rosenfeld 1988; Rumelhart et al. 1986). Each neuron performs an identical, very simple computation over its set of "dendritic" activities before passing on this value via its "axon" to other neurons. Some neurons are initially stimulated, and activity propagates from these throughout the rest of the network via weighted links corresponding to synapses. A "learning rule" must also be defined (e.g., Hebb's correlation rule, back propagation) to govern how synaptic weights change as a consequence of neuronal activity.

Both genetic algorithms and neural networks now represent broad, well-investigated classes of algorithms, with some well-understood computational properties. It is possible to *compose* these two models into a single hybrid system in order to investigate interactions between evolutionary and learning systems (Whitley and Schaffer 1992). For example, variable characteristics of the neural network, including

the number of neurons in the network, the pattern of their interconnectivity, and parameters of the learning rule, can be encoded as allelic values on a genome manipulated by the genetic algorithm. These individuals are selected for some phenotypic characteristic, for example, how effectively the neural networks learn to perform a certain task.

Questions at the heart of the interactions between evolutionary and learned adaptations can be explored using hybrid genetic algorithm/neural network models such as these. For example, a range of "genetically" variable genetic algorithm solutions can be shown to all ultimately converge on the same "phenotypic" neural network solution, due to the plasticity of neural network learning algorithms. Convergence of these networks to a small set of consistent solutions suggests underlying environmental constraints guiding this convergence. Such simulations have been useful in demonstrating important but subtle phenomena, such as canalization and the Baldwin effect, by which effective intra-individual adaptation can speed evolution without Lamarckian-like genetic inheritance of the results of the adaptations (Belew 1990; Hinton and Nowlan 1987). The superposition of computational models of genetic systems and neural learning like this promises to create a new medium for communication between the frequently disjoint communities of population geneticists and neuroscientists with shared interests in behavior.

THE EVOLUTIONARY CONSEQUENCES OF LEARNING

A model system that is often used to assess the evolutionary consequences of learning is vocal learning in songbirds. Song is chosen because it is directly related to mating behavior, it is a well-studied phenomenon, and song learning is a relatively simple behavior that can be assessed at a number of different levels of evolution including morphological, physiological, and behavioral levels. A pertinent question to this area of study is: Does learning of species recognition signals facilitate rapid speciation?

Marler (1990) has demonstrated that songbirds learn to produce and recognize the songs of their species as juveniles. White-crowned sparrows and other songbirds develop a specific song dialect that differs from that of other members of the same species in different geographic locations. Female white-crowned sparrows show behavioral preferences, in the context of copulation behavior, for the song dialect to which they were exposed as juveniles (Casey and Baker 1992). If females select mates on the basis of their songs and prefer males from their natal dialect, then this could potentially foster speciation. White-crowned sparrows may be in the process of breaking up into different species, but the evidence is equivocal. Questions that need to be addressed more rigorously include: Is genetic variance between dialects greater than that within dialects? Do males learn songs in their natal dialect and/or alien dialects? Does either sex disperse away from the natal dialect area before mating?

There are many species in the three groups of birds that learn vocalizations (songbirds, humming birds, and parrots; see Brenowitz, this volume; Kroodsma 1982),

and this provides some indirect support for the hypothesis that learning of species recognition signals may facilitate rapid speciation. Also, there are many more species in the songbird suborder of the Passeriform order that learn song, than in the non-songbird suborder. However, it should be noted that extensive speciation has also occurred in groups of birds that do not learn their species-specific vocalizations (e.g., pigeons, tyrranid flycatchers). Perhaps the degree of speciation that we observe in different groups of birds relates more directly to the general ability of these birds to learn, rather than the specific ability to learn vocal behavior.

CONCLUSIONS

Several conclusions emerged from our discussions of how evolution and behavior interact, probably the most profound of which is that a modicum of "tinkering" at any level of organization (e.g., genetic, molecular, neural) can cause dramatic changes in the behavior of an organism with little change in the anatomical substrate. It is noteworthy that in spite of the conservatism of the nervous system, varying degrees of flexibility at different organizational levels allow the genome to give rise to pronounced degrees of phenotypic variation. The constraints occurring from the molecular level to the levels of behavioral learning act to channel evolution in certain directions, and it is a compromise between the tug of these constraints and the flexibility that allows for evolutionary tinkering that results in the well-adapted, highly variable products of evolution that inhabit the earth.

Behavior shapes the world in which the individual lives and is itself a product of the environment in which it is expressed. It allows the organism to take an active role in its own evolution, to depart ultimately from the constraints of the physiology that fashions it, and to move into perhaps a new level of evolutionary organization called cultural evolution.

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