The evolution of neuronal circuits underlying species-specific behavior

Paul S Katz* and Ronald M Harris-Warrick†

The nervous system is evolutionarily conservative compared to the peripheral appendages that it controls. However, species-specific behaviors may have arisen from very small changes in neuronal circuits. In particular, changes in neuromodulatory systems may allow multifunctional circuits to produce different sets of behaviors in closely related species. Recently, it was demonstrated that even species differences in complex social behavior may be attributed to a change in the promoter region of a single gene regulating a neuromodulatory action.

Addresses
*Department of Biology, Georgia State University, 402 Kell Hall, 24 Peachtree Center Avenue, Atlanta, Georgia 30303, USA;
e-mail: pkatz@gsu.edu
†Department of Neurobiology and Behavior, Cornell University, Seeley G Mudd Hall, Ithaca, New York 14853, USA;
e-mail: rmh4@cornell.edu

Abbreviations

FMRFamide	Phe-Met-Arg-Phe-amide
GABA	γ-aminobutyric acid
GPR	gastropyloric receptor
JAR	jamming avoidance response
NMDA	N-methyl-D-aspartate
STG	stomatogastric ganglion

Introduction

Neuronal basis of species-specific behavior

Natural selection acts on many aspects of organisms, from their appearance to their molecular makeup. Evolutionary pressures also shape the behavior of organisms, producing species-specific behaviors. Although it is a difficult task to determine the neuronal basis for complicated behavior even in a single species, insights into neuronal circuit design can be gained by comparing closely related species with different behaviors. The variations seen between the species' nervous systems could serve as natural experiments for probing the role of those structures in the production of behavior [1]. Furthermore, determining the extent of the differences between the nervous systems of two species with different behaviors can give an indication of how finely tuned nervous systems must be in order to generate appropriate behaviors.

Numerous examples exist showing that neuronal differences can cause changes in behavior between closely related species [2–4]. For example, two closely related species of deer, the white-tailed deer (*Odocoileus verginianus*) and the mule deer (*O. hemionus*) use different gaits when alarmed. The white-tailed deer gallop, whereas the mule deer stot. It can be inferred that this species difference in behavior is caused by genetic differences in the

nervous systems of the two species because hybrid offspring produce an intermediate behavior: they bound when alarmed [2]. Recently, the neural basis for species-specific behavior was dramatically demonstrated by transplanting vocalization-related brain tissue from a Japanese quail to a chicken embryo, and transforming the vocalizations from one species to the other [5••]. Progressive changes in behavior can also be traced in certain lineages in which new behaviors evolved as a series of elaborations of pre-existing specialized behaviors [6•,7,8,9•].

Mechanisms underlying species differences in behavior

Numerous factors might contribute to producing a difference in the behaviors of closely related species. First, the species could differ in their acquisition of sensory signals. There are many examples of elaboration or loss of sensory structures in related species [10,11]. Second, the central neuronal networks of two related species might process information differently. This could involve changes in the number or properties of cells and synapses in the central nervous system or in their pattern of connectivity [12–15]. Finally, the peripheral structures might be modified to respond differently to central commands. Changes in the relative size, position, or number of muscles can produce qualitatively different movements from the same neuronal motor pattern [9•,16,17•].

It has been suggested that because peripheral structures are subject to fewer constraints, they might be more likely than central circuits to exhibit phylogenetic differences ([12–14,18]; see, however, [19]). However, general properties of the nervous system and specific developmental mechanisms serve to keep the nervous system matched to a changing periphery. For example, a change in the size of sensory or motor structures will induce a corresponding change in the number of central neurons that serve that structure [20,21]. In addition, some changes in sensory input can be automatically accepted by existing neuronal circuits without necessarily inducing any central changes [22••]. In this review, we will focus primarily on how cellular changes to central neuronal networks may mediate the evolution of species-specific behaviors.

Are neurons conserved through evolution?

The basic organization of nervous systems tends to be highly conservative. Members of species belonging to the same genus often have almost indistinguishable nervous systems. In invertebrates, where individual neurons can be unambiguously identified from animal to animal within a species, homologous neurons can be identified in disparate members of a taxon such as Insecta [23] and even across phyla [24•]. Of course, homologous neurons

can exhibit certain morphological modifications that are taxon specific [25].

Homologous neurons in disparate species also can be identified by neurochemical criteria. For example, homologous serotonin-immunoreactive neurons can be identified in highly divergent species within the class of gastropod molluscs [26]. Similarly, in the class Crustacea, serotonergic neurons that have been identified in highly derived decapod species such lobsters and crayfish [27] are also found in primitive anaspid species such as *Anaspides tasmaniae* [28]. Although there are important examples of prominent neurons that have been lost during evolution in some members of a lineage [29], our impression is that identified neurons are often conserved during evolution.

The most common difference seen in closely related species is a change in the number of cells of a particular type [14,30,31•,32,33,34•]. The organizational features of some neuronal structures, such as the laminar organization of neuronal cell types (e.g. as in the cerebral cortex, the retina, and certain nuclei), provide a simple mechanism for addition or subtraction of identical units, leading to computationally important changes in neuronal number [35•,36].

Is circuit organization conserved through evolution?

Not only can individual homologous neurons be identified across species within a phylum but, as might be expected, entire circuits are conserved, even across phylogenetic orders. For example, the basic organization of the central pattern generators for locomotion is conserved in a variety of vertebrate spinal cords, including the spinal cord of lamprey, larval *Xenopus*, and neonatal rat [37•]. However, differences in the detailed cellular properties of spinal neurons and the amount of excitatory input that they receive have been noted, even between closely related species [38•,39]. Similarly, many of the same connections are found between homologous neurons underlying escape swimming in two molluscs of the subclass Opisthobranchia: the nudibranch *Tritonia diomedea* and the notaspid *Pleurobranchaea californica* [40•].

The complexity of the nervous system makes it difficult to determine the extent of phylogenetic differences in neuronal circuits. Therefore, work on the numerically simple crustacean stomatogastric ganglion (STG), which contains just 30 neurons, has been enlightening. The neuronal circuitry of the STG has been remarkably well preserved over at least 350 million years of evolutionary divergence, despite radical changes in the peripheral structures that it controls [15,41••,42–44]. Most of the neurons in the pyloric network are identifiable in all species, though the numbers of some of the cell types can vary. The overall synaptic circuitry is similar, but there are differences in the relative strength of particular synaptic connections and the amount of electrical coupling between neurons in different species [41••,43,44,45•]. In some species, the intrinsic properties of

individual neurons have diverged, causing similar circuits to produce different motor patterns [42,43,46]. Most of the identified neurons have retained their transmitter phenotype across species; however, in one more distantly related species, the transmitter of two neurons is different but the postsynaptic ionic response to those neurons has remained the same as in the other species [47].

Constraints attributable to multifunctional networks

One possible reason that neural networks are so well preserved across species is that neuronal circuits act as generalists rather than specialists: a single motor circuit can produce a variety of different motor patterns under different circumstances [48–53] or at different times during the development of the animal [54–57]. These different behavioral outputs depend upon the actions of neuromodulatory inputs, as well as sensory feedback. Modulatory inputs can reconfigure networks by altering the strength of synapses and changing the intrinsic firing properties of the component neurons through the release of substances such as amines and neuropeptides [52,58]. In addition, modulatory inputs can cause neurons to switch allegiance from one network to another and, in some cases, can cause the fusion of multiple independent networks into a single conjoint network controlling a complex behavior [48,59–63]. This flexibility in the output of neuronal networks has two evolutionary consequences. First, there is no need to evolve a completely new circuit to produce a new behavior. Second, the fact that a network must play roles in many different behaviors or at different developmental stages may constrain it from being altered because changes in the network that would be advantageous for one behavior might be disastrous for another.

Changes in the input to a circuit

If neuronal circuitry evolves more slowly than behavior, then perhaps natural selection can alter the range of behaviors produced by a circuit by changing its inputs or by changing how it handles those inputs. Furthermore, it may be more parsimonious to alter the inputs to a circuit than to change the connectivity within a circuit itself. The electrosensory system in South American electric fish provides an excellent example of behavioral differences arising from differences in the inputs to similar circuits. The pacemaker nucleus underlying the jamming avoidance response of the two closely related South American electric fish genera, *Eigenmannia* and *Apteronotus*, is similar. However, the nucleus receives different sets of inputs from other brain areas that cause a different behavioral response in the two species [64,65•]. Variations in the inputs to circuits have been shown to play a role in the expression of species-specific behavior in tadpoles [66–68], and species differences in the aminergic input to the mammalian cerebellum have also been reported [69]. In addition, many phylogenetic variations have been observed in the neuromodulatory inputs to the STG [15]. For example, serotonergic innervation of the STG is

provided by a set of muscle receptor neurons that have been identified in at least eleven species from six decapod crustacean infraorders. There are species and lineage differences in the number of these neurons (varying from one to four pairs), the muscles that they innervate, and their apparent peptide co-transmitters (e.g. allatostatin-, cholecystokinin-, and FMRFamide-like immunoreactivity) [70•,71–73]. Furthermore, in the spiny lobsters, the neurons are present, but they do not contain serotonin [74]. Instead, serotonin is thought to be delivered as a circulating neurohormone. Species differences in the mode of delivery of a neuromodulatory substance, including release from different neurons with different co-transmitters and targets in the network, could dramatically alter the role that the compound plays in the production of behavior [71,75,76,77•].

Changes in responses and receptors

The response of particular neurons or brain areas can change even if the transmitters involved stay the same [53,74,78]. For example, serotonin is known to have two effects on sensory neurons in the mollusc *Aplysia californica* that play a role in non-associative learning: it increases their excitability and causes spike broadening. However, in other related species, the spike broadening response is absent [79]. This may be attributable to differences in the types of serotonin receptors on these identified neurons or the coupling of the receptors to their second-messenger systems. In one species, both the spike broadening and excitability responses are absent, and this species also lacks dishabituation and long-term sensitization in the tail withdrawal reflex, which are thought to be mediated by serotonin in *Aplysia* [80].

Changes in receptor type or distribution can lead to marked changes in behavior. A particularly striking example of this is seen in two species of voles that differ in their affiliative behavior. The prairie vole (*Microtus ochrogaster*) forms monogamous pair bonds, whereas the montane vole (*Microtus montanus*) is solitary and does not show a preference for former mates. Two peptide transmitters, oxytocin in the female and vasopressin in the male, are responsible for the pair-bonding behavior in prairie voles [81]. The pattern of oxytocin and vasopressin immunoreactivity in the brains of the two species does not differ substantially, but the distribution of their receptors does [82,83•]. Furthermore, the gene for the vasopressin receptor differs in its 5′-flanking region but not in the coding region [84••]. This difference may determine which regions of the brain express the receptor. A transgenic mouse expressing the prairie vole vasopressin receptor gene shows a pattern of vasopressin receptor expression that is similar to that seen in the prairie vole, and increased affiliative behavior in response to vasopressin, also reminiscent of prairie voles [84••]. This work demonstrates that the localization of receptors that underlie differences in behavior can be accomplished easily through mutations in the promoter regions of particular genes.

Importance of knowing phylogeny

When comparing the neuronal circuitry underlying behaviors in two species, it is important to understand the phylogenetic relationships between the species and to conduct an out-group comparison. For example, by comparing the neuronal responses to serotonin with a phylogeny based on other characters, it was shown that the lack of a sensory neuron excitability response in the mollusc *Dolabrifera* was attributable to a secondary loss of the response after splitting from other groups that retained it [79]. Another good example is work on the jamming avoidance response (JAR) in weakly electric fish. Electroreception arose early in vertebrate evolution and was subsequently lost and 're-evolved' numerous times [85]. Two different genera of wave-type electric fish both evolved a JAR to prevent their electric signals from being confused with similar signals from nearby fish [86,87]. This behavior has very particular requirements, and thus both species use an identical set of computational rules to perform the task. However, the circuitry underlying these apparently identical behaviors resides in different brain areas, revealing that the two behaviors evolved independently [88].

Conclusions

Although nervous systems tend to be more evolutionarily conserved than other parts of the body, centrally generated behavioral patterns do change. It appears that rather subtle changes in the nervous system can cause large and important changes in the behavior of an organism. This fits very well with our understanding of how neuronal circuits and even single neurons can show dramatic alterations in activity with very small changes in parameters such as the density of ion channels [89]. The modulatory inputs to neural networks seem to be a very plastic trait in CNS evolution. A change in the distribution of receptors or in the expression of peptide co-transmitters can be made very easily through changes in the promoter regions of the genes. The nervous system is organized in such a way that it can accept these changes and incorporate them to generate a novel species-specific behavior.

Acknowledgements

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Chickens (*Gallus gallus domesticus*) and Japanese quail (*Coturnix coturnix japonica*) exhibit species-specific vocalizations that include complex head movements. It was found that transplanting regions of the midbrain or brain-stem from the embryo of one species to the other could transform the adult behavior of the host species, causing it to express components of the behavior exhibited by the donor species. These results are interpreted to mean that species differences in behavior are attributable to localized changes in the neuronal circuitry.

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