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Diversity Matters

The Importance of Comparative Studies and the Potential for Synergy Between Neuroscience and Evolutionary Biology

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Basic research in neuroscience and clinical research on neurological disorders synergistically increase our understanding of the human brain. Traditionally, functional and clinical studies of the human brain were limited to postmortem histology, "natural experiments" (eg, lesions to brain areas caused by trauma or disease), and crude measures of electrical activity such as electroencephalography. More recently, the development of transcranial magnetic stimulation and rapid advances in imaging technology have greatly facilitated human brain research. In rare cases in which treating a neurological disorder involves implanting electrodes, researchers can even record the electrical activity of individual neurons. Although these approaches have led to important insights, they do not allow for a precise dissection of the underlying mechanisms by which the brain mediates perception, cognition, and behavior. Thus, neuroscientists and neurologists remain severely limited in the types of experiments they can perform on human subjects and much of our understanding of brain structure and function is based on research in animal models. In this article, I highlight the enormous potential for synergy between neuroscience and evolutionary biology. Nervous systems have been shaped by evolution, and comparative approaches take advantage of the resulting diversity to gain insight into the neural mechanisms of behavior. On the other hand, nervous systems and the behaviors and perceptions they mediate can play a fundamental role in the evolutionary processes that generate this diversity. To emphasize these points, I describe recent findings from research on African fishes that use electricity to communicate and navigate in their dark underwater world.

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The most important consideration in choosing a model system is that it should allow for the development of broadly applicable principles relevant to all nervous systems. Neuroscientists have followed at least 4 nonexclusive strategies in selecting model systems: (1) choosing organisms that are convenient for laboratory study (convenient model systems approach), either because they are easy to house, care for, and breed or because certain characteristics make their nervous systems more accessible, such as having large identified neurons or transparent embryos; (2) choosing organisms for which precise genetic manipulations are possible (genetic model systems approach); (3) choosing organisms based on their relatedness to humans (anthropocentric model systems approach); or (4) choosing organisms that are particularly well suited to studying the neural basis of specific behaviors (neuroethological model systems approach). Each approach has its own advantages and disadvantages. As a result, the history of neuroscience is replete with studies on diverse species that

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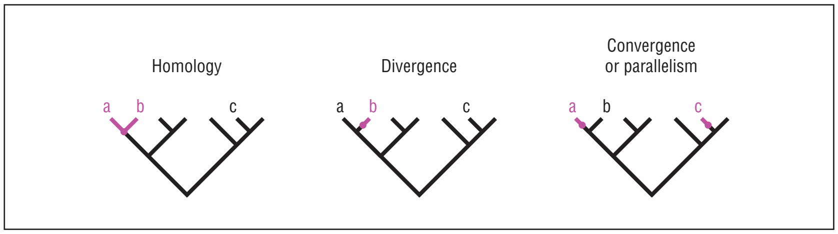

Figure 1. Traits can evolve in a variety of ways that give rise to different patterns of trait distribution across species. In each case, a phylogenetic tree shows evolutionary relationships among extant (ie, living) species with the ancestral trait represented by black branches and the origin of a novel trait represented by colored circles that give rise to colored branches. *Homology* describes a trait that is shared among related species owing to descent from a common ancestor, which in this case causes the closely related species a and b to share a novel trait that is lacking in the distantly related species c. *Divergence* describes the evolution of trait differences between related lineages, which in this case causes species b to have a novel trait that is lacking in the closely related species a as well as the distantly related species c. *Convergence* and *parallelism* both describe the evolution of similar traits in unrelated lineages, which in this case causes species a to have a novel trait that is also found in the distantly related species c but lacking in the closely related species b. *Convergence* describes the independent evolution of a novel trait from unrelated ancestral traits, whereas *parallelism* describes the independent evolution of a novel trait from the same ancestral trait.

have played an essential role in the development of basic principles of neural structure, function, and development.[1,2] In recent years, however, neuroscientific research has become increasingly focused on a limited number of model systems, as genetic tools and anthropocentric perspectives have taken precedence over other considerations.[2] Such an extreme bias limits the scope of potential discoveries and the identification of new model systems for studying particular functions and dysfunctions.

COMPARATIVE APPROACHES TO NEUROSCIENCE

Many neuroscientists study primates because of their relatively close evolutionary relationship to humans (ie, anthropocentric model systems approach). Rodents are used far more widely,[2] since they are much easier to house and study (ie, convenient model systems approach) and, in the case of mice, a wealth of genetic tools is available (ie, genetic model systems approach). Despite being more distantly related to humans than are primates, rodents are still mammals; from an anthropocentric perspective, this gives them an edge over other genetic model systems (eg, *Drosophila* or *Caenorhabditis elegans*). The implicit assumption of the anthropocentric approach is that degree of evolutionary relatedness reflects degree of similarity; thus, in studying the brain of as close a relative to humans as possible, one is studying a brain that is as similar to humans as possible. However, the evolutionary process is not so simple (**Figure 1**). Traits can be shared among closely related species owing to descent from a common ancestor (ie, homology), but they can also diverge among closely related species, and some traits may actually be unique to a given lineage. Further, similar traits can arise independently in unrelated lineages (ie, convergence or parallelism). Thus, although the overall degree of similarity between species may correlate with the degree of relatedness, this general rule does not hold for each particular trait, and studying a closely related species may provide insight into the neural basis for some behaviors, but not others. For example, songbirds, parrots, hummingbirds, bats, and whales are, to date, the only animals other than humans known to produce learned vocalizations.[3] Songbirds have therefore served as a powerful model for studying mechanisms of vocal learning, providing insights into human language acquisition that only species with this behavioral capability could provide.[3]

Brains, like all traits, are enormously diverse. As with any biological trait, nervous systems are adapted to the environments in which they evolved, having been sculpted by natural selection to extract information from that environment and to use that information to perform behaviors that maximize survival and reproduction. From a neuroethological perspective, a complete understanding of brain function requires an appreciation for the natural environment to which an animal's nervous system is adapted, including the sensory inputs it receives and the behaviors it performs in that environment. The neuroethologist Fernando Nottebohm said it well:

> Unless you understand the needs, the habits, the problems of an animal in nature, you will not understand it at all. Put rats and mice into little plastic boxes and you will never fully comprehend why they do what they do. Take nature away and all your insight is in a biological vacuum.[4(p53)]

Indeed, Nottebohm overturned decades of scientific dogma when he revealed adult neurogenesis in the brains of canaries, a discovery that stemmed from selecting a model organism based on its natural behavior (open-ended song learning) rather than its relatedness to humans or the availability of genetic tools. Although many were skeptical of the general relevance of this finding at the time, adult neurogenesis has since been documented in rodents and primates.

The unifying theme of neuroethology is a focus on behavior in its natural context.[1] If the ultimate goal of neuroscience is to understand neural mechanisms of behavior, then studying species that perform similar behaviors, or even those that are exceptionally skilled at those behaviors, can provide important insight into those mechanisms. Comparative biologists seek to identify correlated evolutionary change in 2 or more traits as a means to identify traits that may be causally related. Comparative approaches in neuroscience can therefore be used to identify behavioral traits and neural traits that covary across species and thereby identify both possible candidate mechanisms for a behavior, as well as model systems for studying those mechanisms in greater detail. Comparative approaches can also be used to test existing mechanistic hypotheses. For example, if a specific brain region is thought to be important for a particular behavior, then behavioral differences between species should correlate with variation in this region. This view is embraced by the emerging field of neuroecology, which capitalizes on the neuroethological approach to choosing model organisms for studying the neural mechanisms of behavior and applies ecological principles to determine how these behavioral mechanisms shape interactions among individuals, populations, species, and communities.[5] This approach seeks to identify how natural selection acts as a driving force shaping the evolution of brain structures, perception, cognition, and behavior to adapt organisms to their environments.

A recent study of African fishes of the family Mormyridae provides a clear example for how correlated evolutionary change between a behavioral and neural trait can provide evidence for a mechanistic link.[6] Mormyrids have a specialized electric organ that generates relatively weak pulses of electricity.[7] They use these electrical pulses both to communicate with each other and to actively sense their environment.[7] In 2 separate lineages of these fishes, a brain region devoted to processing electric communication signals expanded in size and divided into 2 distinct subregions.[6] Behavioral experiments revealed that species in both lineages are able to detect subtle variation in the waveform of these electric pulses, whereas species in other lineages are not, providing evidence for a link between sensory perception and neural circuitry.[6] This perceptual ability relies on the detection of submillisecond differences in the timing of synaptic inputs, and ongoing studies are directly targeting the underlying mechanisms that make this perceptual ability possible. This will not only reveal how these particular fish analyze these particular communication signals; importantly, it will reveal mechanisms by which any neural circuit can detect slight variation in the temporal structure of sensory stimuli, which plays an important role in sound localization and speech comprehension in humans.[8] As the physiologist August Krogh stated,

> For such a large number of problems there will be some animal of choice or a few such animals on which it can be most conveniently studied.[9(p247)]

Indeed, some of the most fundamental principles in neuroscience arose from research on a wide variety of species, each chosen for their unique experimental advantages (**Table 1**). Some may counter that comparative studies have certainly been important historically but that modern genetic tools have rendered this approach obsolete. However, relatively recent, broadly significant discoveries such as how auditory maps of space are calibrated by visual experience in barn owls, the effects of neuromodulators in reconfiguring motor patterning in crustaceans, and the role of sleep in memory consolidation in songbirds suggest otherwise.[1] The availability of genetic tools makes mice a powerful model system for addressing many, but certainly not all, questions in neuroscience. Can the visual system of a burrowing, nocturnal rodent really be considered an appropriate model for studying the neurobiological basis of human visual perception?

Table 1. Diverse Models Systems Have Played a Fundamental Role in the Advancement of Neuroscience[a]

Model System	Insight
Squid	The ionic basis of the action potential
Aplysia	Understanding of the cellular basis for learning and memory
Chicken	Discovery of nerve growth factor
Caenorhabditis elegans	Discovery of programmed cell death (apoptosis)
Chicken	Discovery of dendritic spines
Monkey	Discovery of radial neuronal migration
Canary	Discovery of adult neurogenesis and neuronal replacement
Horseshoe crab	Discovery of visual receptive fields and lateral inhibition
Barn owl	Discovery of computational maps of auditory space
Cat and monkey	Understanding of cortical columnar organization and development
Frog	Discovery of the reflex arc
Lamprey	Understanding of spinal cord circuitry for locomotion
Monkey	Discovery of dopaminergic reward signaling
Dog	Discovery of conditioned reflexes
Pigeon	Discovery of operant conditioning

[a] This nonexhaustive list provides several examples of how findings from comparative neuroscience research have fostered the development of basic principles (see Marder[1] and Manger et al[2] for additional information).

NERVOUS SYSTEMS AS FUNDAMENTAL DRIVING FORCES IN EVOLUTION

While neuroscientists can take advantage of species diversity to study neural mechanisms of behavior, the nervous system itself can actually play an important role in generating this diversity. Darwin referred to the origin of new species as "that mystery of mysteries."[10] Even today, the process of speciation remains one of the most hotly contested areas of evolutionary biology.[11,12] The biological species concept defines species as groups of naturally occurring interbreeding populations that are reproductively isolated from other such groups.[11,12] Reproductive isolation can come in many forms but is generally subdivided into factors that prevent mating between individuals (premating isolation), those that prevent fertilization after mating (postmating isolation), and those that result in abnormal development or sterility after fertilization (postzygotic isolation).[11]

The most widely accepted evolutionary scenario is that of allopatric speciation, in which a population becomes subdivided into geographically isolated populations owing to dispersal or geologic processes.[11] The effects of natural selection in these dissimilar environments, as well as the random occurrence of different mutations and genetic drift, can all produce genetic divergence between these populations that ultimately leads to reproductive isolation. More contentious is the process of sympatric speciation, in which new species evolve from an ancestral species within the same geographic region.[11] Such a process could result

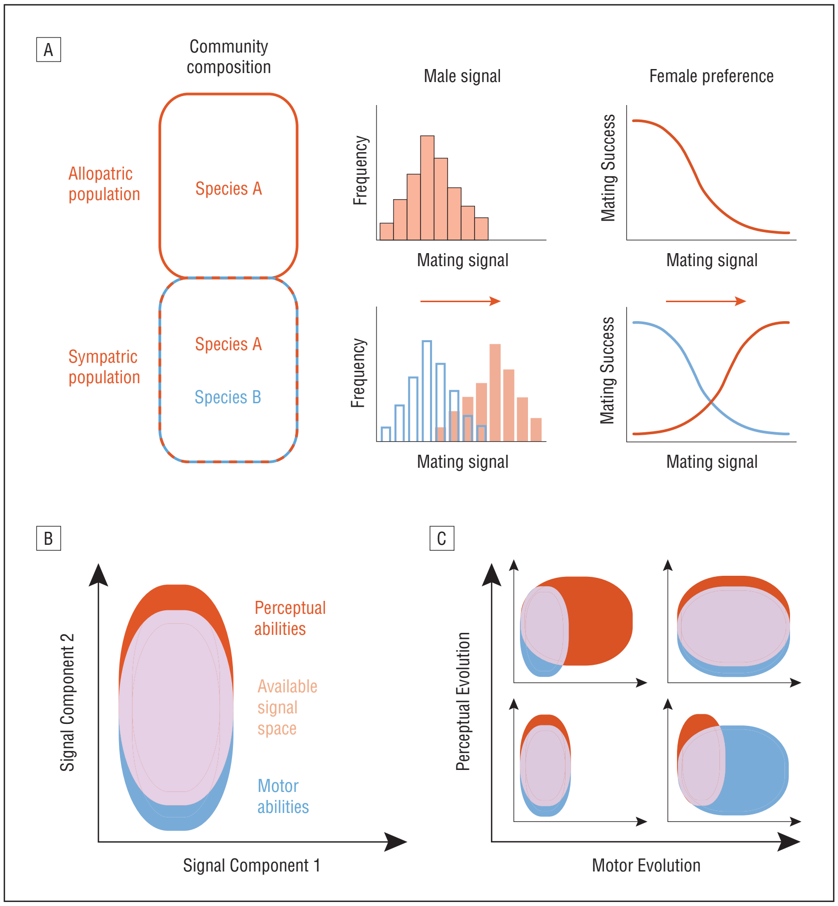

Figure 2. Animal communication and its role in species diversification. A, Species interactions and communication signals can lead to speciation. In this example (modified from Hoskin et al[13]), one population of species A is geographically isolated from species B (allopatric) whereas another overlaps geographically with species B (sympatric). Histograms show the distribution of a mating signal (eg, call rate) across males in the population, and the curves show the variation in mating success of males as a function of signal variation due to female preferences for certain signals. Similarity between the mating signals of 2 species can cause the male signal and female preference for that signal to shift in areas of sympatry (red arrows), a phenomenon known as reproductive character displacement. This shift results in 2 populations of species A having different male signals and female preferences, which can lead to reproductive isolation between the 2 populations and the formation of 2 different species. B, Communication signals often have several different components that can be visualized within a multivariate signal space in which each dimension corresponds to a different signal component, eg, call duration and call rate. The signal space available for communication is limited by the intersection of sender motor abilities and receiver perceptual abilities. C, Evolutionary change in sender motor abilities and receiver perceptual abilities can expand the available signal space.

from disruptive selection, in which intermediate traits are selected against, leading to diverging populations that lie at the extremes. Although geographic context is important, the spatial relationships of populations are often complex, and many other factors can influence gene flow among populations.[12] In particular, communication signals are critical for species recognition and mate choice and can therefore play a fundamental role in both the generation and maintenance of species diversity through their effects on premating reproductive isolation.[12,13] In populations that have already partially diverged as a result of adaptation to different environments, selection against the production of hybrid offspring that are poorly adapted to either environment can drive divergence of both mating signals and signal preferences when choosing mates. Thus, signal divergence can reinforce ecological divergence and thereby accelerate the process leading to complete reproductive isolation. Signal variation, by itself, can also directly promote speciation.[13] Random mutations and genetic drift can lead to signal divergence between allopatric populations even in the absence of any ecological divergence. If the signals and preferences for those signals have diverged enough, then they can mediate premating isolation on secondary contact between those populations. Adaptations for maximizing signal transmission in different environments can also lead to signal divergence and reproductive isolation.[14] In addition, interactions between species can promote signal divergence that leads to reproductive isolation.[13] For example, one species may partially overlap with other related species throughout its geographic range. Signal divergence to avoid hybridization in areas of overlap can cause signals and preferences to diverge, leading to reproductive isolation from other populations of the same species (**Figure 2**A).

Communication signals can vary in several respects. For example, acoustic communication signals can vary in their spectral characteristics (eg, dominant frequency, number of frequency bands, and bandwidth), temporal characteristics (eg, duration, rate, interval, rise time, and decay time), and intensities. Further, covariation in these different features provides additional possibilities for signal variation (eg, relative amplitudes of harmonics or side frequencies and amplitude or frequency modulation). This variation can be conceptualized as a multidimensional "signal space" in which each signal occupies a distinct location within that space. However, the available signal space is limited by the motor ability of senders to generate different signals, as well as the perceptual ability of receivers to detect different signals and discriminate among them (Figure 2B), thereby limiting the possible extent of signal divergence.[7] On the other hand, evolutionary change in perceptual or motor abilities can expand the available signal space (Figure 2C), and entirely new dimensions can be made available by the evolution of completely novel sensory or motor abilities.[7] These new abilities could arise owing to selection acting directly on communication systems, or they could evolve in response to unrelated selection pressures. For example, trichromatic color vision may have evolved from dichromatic vision in primates as an adaptation to distinguishing fruits from leaves, or leaves of different ages, while foraging.[15] Regardless of the ultimate cause, sensory or motor evolution can drive species diversification because the enlargement of available signal space provides more room for more species to occupy distinct regions within this space.

Evolutionary change in the inner ear of frogs has been linked to increased diversification through its effects on the perception of vocal communication signals.[16] The adaptation of photoreceptors to different light environments has led to speciation in African cichlid fishes.[17] Song-learning ability may have increased speciation rates in songbirds.[18] Likewise, the evolution of a new perceptual ability to detect the fine temporal structure of electric communication signals in mormyrid fishes led to a 10-fold increase in the rate of signal evolution and a 3- to 5-fold increase in the rate of species diversification.[6] However, this dramatic increase in diversification only occurred in the lineage that had also evolved a motor ability to generate variation in the fine temporal structure of electric signals. Lineages of these fishes that evolved only the perceptual or motor ability alone did not experience this rapid increase in signal and species divergence. Thus, evolutionary change in both perceptual and motor abilities may be necessary for an expansion of signal space that can trigger increases in signal and species divergence (Figure 2C). However, evolutionary changes in sensory and motor abilities are not by themselves sufficient to trigger increased species diversification, which is most likely to occur when these novel abilities are directly related to the production or detection of signals that are involved in species recognition and mate choice.[7]

Evolutionary change in nervous systems can also drive species diversification by mediating ecological adaptation.[7] The evolution of passive and active electrolocation in fishes and echolocation in bats provide clear examples of how novel sensorimotor abilities can permit the use of new ecological niches. The expansion of the available "ecological space" can then fuel diversification as different species specialize on distinct niches within this space.[11,12] In some cases, a single trait may be involved in both ecological adaptation and species recognition, and these so-called magic traits can greatly facilitate speciation.[7,12] It is clear that a variety of evolutionary processes can result in distantly related species occupying the same sensorimotor space, and closely related species occupying a distinct space, underscoring the need to choose model systems based on the behavior of interest rather than relatedness.

Table 2. Different Questions in the Study of Behavior[a]

Causal Level	Question	eg, Why Do Songbirds Sing?
Ultimate	Evolutionary history	Song arose early during the evolution of oscine birds
	Adaptive function	To attract mates and defend their territory from rivals
Proximate	Mechanisms	Because of steroid hormones acting on song regions of the brain
	Development	Because they learn song from an adult tutor during a critical period

[a] Mayr identified 2 distinct levels of analysis in biology, an ultimate level of analysis that refers to evolutionary causes and a proximate level of analysis that refers to causes within the organism's lifetime. Tinbergen identified 4 different questions in the study of behavior: evolutionary history and adaptive function relate to ultimate levels of analysis, whereas mechanisms and development relate to proximate levels of analysis.[19] Here, birdsong is used as an example of how addressing these 4 questions can give rise to nonmutually exclusive hypotheses.

AN INTEGRATIVE APPROACH TO BRAIN, BEHAVIOR, AND EVOLUTION

Based on Ernst Mayr's distinction between ultimate (ie, evolutionary) and proximate (ie, mechanistic) causes in biology, the ethologist Niko Tinbergen identified 4 distinct questions related to any particular behavior[19]: What is the evolutionary history of the behavior? What is the adaptive function of the behavior? What is the immediate mechanism of the behavior? How does the behavior develop throughout the life of the animal? Importantly, these different types of questions reveal that a behavior can be explained from several nonmutually exclusive perspectives (**Table 2**). The pitting of hypotheses that address one question against hypotheses that address another can therefore lead to false debate, with proponents of different hypotheses arguing past each other.[19]

Because of the problems inherent to confusing different questions, several have cautioned against integrative approaches to behavior that consider multiple perspectives, while others have championed exactly this type of approach.[19] In my view, a full understanding of behavior requires an integrative approach that considers all 4 of these different questions. Although one must be careful not to confuse different questions about the same behavior, an integrative approach can be deeply informative in addressing them.[19] Indeed, many of the early ethologists studied animal behavior from multiple perspectives because they believed that to do otherwise would result in incomplete, and thus potentially incorrect, explanations for behavior.

Neuroscientists study the inner workings of nervous systems at a variety of levels, from genes to proteins, cells to synapses, and circuits to behavior, with tools from a variety of disciplines. From a behavioral perspective, the underlying insights all relate to component mechanisms for processing sensory input and generating behavioral output (**Figure 3**). Thus, the function of a behavior describes how these mechanisms mediate adaptive interactions with the environment, and these interactions have fitness consequences that determine how variation across the population leads to differential survival and reproduction through natural selection. In turn, these fitness consequences result in changes in gene frequencies over time, ultimately leading to evolutionary change in the underlying mechanisms for behavior, the realization of new behavioral functions, and changes in the environment (Figure 3). Viewed from this embedded, integrative perspective, an understanding of adap-

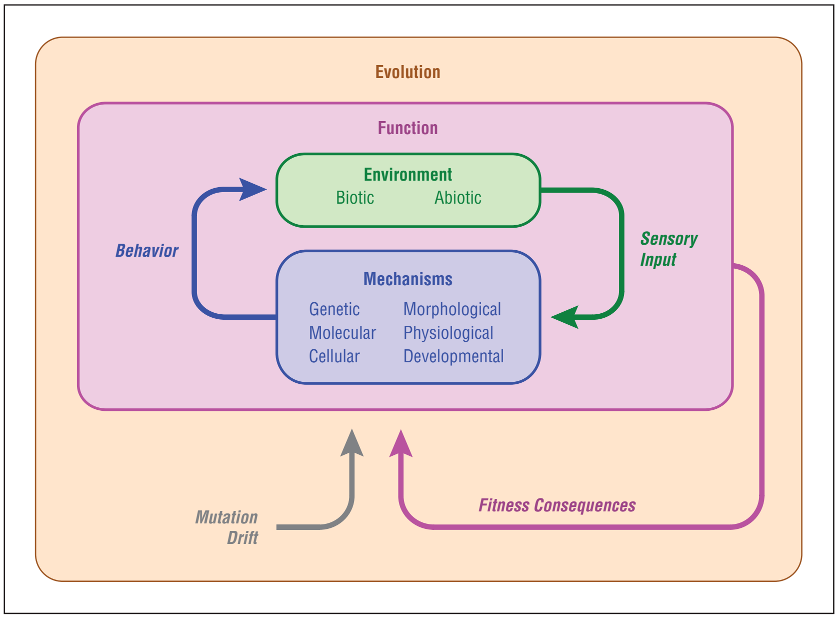

Figure 3. An integrative approach to the study of brain, behavior, and evolution. Neural mechanisms can be studied at a variety of levels, from molecular genetics to neural systems. From a behavioral perspective, all of these mechanisms relate to the processing of sensory input from the environment and the generation of behavioral output. Function describes the adaptive significance of these interactions, or the ways in which these interactions enhance survival and reproduction. Functional variation therefore has fitness consequences that result in differential survival and reproduction within populations, the process known as natural selection. These fitness consequences, combined with random processes such as mutation and drift, result in changes in gene frequencies within populations, leading to evolutionary change in neural mechanisms and environments, as well as functional interactions between the two.

tive function can guide the development of mechanistic hypotheses, define the categories of behavior that are explored at a mechanistic level, and set specific criteria that any mechanistic hypothesis must satisfy.[5,19] Further, the development and exploration of mechanistic hypotheses can reciprocally guide the development and exploration of hypotheses about adaptive function and evolutionary history.[19]

The recent demonstration that brain evolution in mormyrid fishes led to increased rates of signal evolution and species diversification provides an example of how hypotheses that address one perspective can inform hypotheses that address another.[6] Previous studies had clearly implicated the electric signals of these fishes as playing important roles in species recognition and mate choice, and this functional perspective on electric signals motivated the search for mechanisms underlying the detection and discrimination of these signals.[7] The identification of specific sensory receptors and brain regions involved in signal processing motivated comparative studies that revealed differences in these neural substrates across species, as well as the history of evolutionary change responsible for this pattern of species variation.[6] Because of the existing understanding of signal processing mechanisms, these species differences immediately suggested that species in certain lineages are unable to detect variation in electric signal waveform. Confirmation of this hypothesis then led to the functional hypothesis that electric signal waveform is not used for species recognition and mate choice in these lineages, which culminated in the evolutionary history hypothesis that these lineages have experienced relatively low rates of signal evolution and species diversification.[6] Although answering a question from one perspective cannot provide answers to questions from other perspectives, clearly they can motivate those questions and guide the development of hypotheses to address them.

THE FUTURE OF COMPARATIVE NEUROSCIENCE

It was nearly 40 years ago that Jerison[20] proposed that the relative size of brain regions is directly related to the information processing capabilities of those regions and therefore the contribution of those regions to behavioral and perceptual capabilities. Although this basic principle largely holds, it has become clear that the detailed cellular and network architecture of the underlying circuits are also critically important in determining information processing. Although the overall size of the human isocortex is impressive, the actual number of cortical neurons and the synaptic interactions among them distinguish the human brain from the brains of other vertebrates to an even greater degree. Comparative studies have contributed much to a basic understanding of the relationship between brain and behavior, but they generally continue to focus on relatively crude measures such as the overall size of particular brain regions, or the total number of neurons, and their relationship to behavior.

The tools available for studying the nervous system at all levels continue to expand, in animal models as well as in humans. As next-generation sequencing costs decline, a wide diversity of species is being added to the list of complete genome sequences. Genetic tools should therefore become available in an increasingly diverse array of species. Computational methods for analyzing genetic data, testing hypotheses about neural mechanisms, establishing evolutionary relationships, and performing quantitative comparative analyses of traits are becoming increasingly sophisticated. Together, these advances offer the promise of performing detailed and extensive comparative studies of nervous systems, thereby identifying the behavioral functions and evolutionary histories of specific genetic, molecular, cellular, synaptic, and circuit mechanisms.

Like all species, our distinctiveness results from both unique traits as well as from unique combinations and modifications of traits that are found in other species. Thus, comparative approaches that study organisms well suited to uncovering the neural basis of particular behaviors ultimately hold the promise of identifying key components of human brain function. Our current understanding of neurodevelopmental and neurodegenerative disorders would be nonexistent without the solid foundation of basic neuroscience that has developed over decades of research on a wide diversity of animals. It is easy to appreciate this in hindsight but much more difficult to predict how this foundation might best be expanded in the future and how this expansion will impact our understanding of both normal and diseased human brains. Studying a diversity of model systems and using a variety of approaches offer the greatest hope of realizing the full potential for discovery.

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