REVIEW

Progress in the Study of Brain Evolution: From Speculative Theories to Testable Hypotheses

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Darwin's theory of evolution raised the question of how the human brain differs from that of other animals and how it is the same. Early students of brain evolution had constructed rather grand but speculative theories which stated that brains evolved in a linear manner, from fish to man and from simple to complex. These speculations were soundly refuted, however, as contemporary comparative neurobiologists used powerful new techniques and methodologies to discover that complex brains have evolved several times independently among vertebrates (e.g., within teleost fishes and birds) and that brain complexity has actually decreased in the lineages leading to modern salamanders and lungfishes. Moreover, the old idea that brains evolved by the sequential addition of new components has now been replaced by the working hypothesis that brains generally evolve by the divergent modification of preexisting parts. Speculative theories have thus been replaced by testable hypotheses, and current efforts in the field are aimed at making phylogenetic hypotheses even more testable. Particularly promising new directions for comparative neurobiology include (1) the integration of comparative neuroanatomy with comparative embryology and developmental genetics in order to test phylogenetic hypotheses at a mechanistic level, (2) research into how evolutionary changes in the structure of neural circuits are related to evolutionary changes in circuit function and animal behavior, and (3) the analysis of independently evolved similarities to discover general rules about how brains may or may not change during the course of evolution. ***Anat. Rec. (New Anat.) 253:105–112, 1998.*** **© 1998 Wiley-Liss, Inc.**

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Origin of man now proved. — Metaphysics must flourish. — He who understands baboon would do more toward metaphysics than Locke.
Charles Darwin, M Notebook, 1838

After Darwin published his *Origin of Species* in 1859, the idea that humans descended from animal ancestors gradually but inexorably gained widespread acceptance. As a result, scientifically educated people found it increasingly difficult to accept the prior notion (defended by John Locke, for example) that the human mind is completely separate from the animal mind and functions according to very different principles. As Darwin's theory of evolution thus forced a reevaluation of man's relationship to other animals, speculation about the evolution of the human mind indeed flourished, as Darwin had predicted in the passage quoted above. Because the brain was by then widely regarded as the anatomical organ that controls both mind and behavior, speculation about brain evolution similarly began to proliferate shortly after the publication of Darwin's book. Within this context, *The Journal of Comparative Neurology* was founded by Charles J. Herrick in 1891, and the first textbook of comparative neurology was published by Ludwig Edinger at the turn of the century.

Despite this increasing interest in brain evolution, the field of comparative neurology was, from the outset, plagued by the fact that neither brains nor behaviors are preserved in the fossil record. This absence of a fossil record for brains and behaviors led to the widespread but mistaken belief that ideas about brain evolution must always remain speculative. Even today, most textbooks of neuroscience present the field of comparative neurology as an interesting but marginal and rather speculative area of inquiry. As a result, few people realize that the field of comparative neurobiology has changed dramatically from its speculative beginnings and has created ever more testable hypotheses. In fact, many of the theories still mentioned in the textbooks of today have already been disproven by contemporary comparative neurobiologists.

The primary aim of this review, therefore, is to chronicle some of this scientific progress in the field of com-

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parative neurobiology. Additional progress will need to be made, of course, but the field currently finds itself at the brink of an exciting new era in which long-standing problems may be resolved by the application of new techniques and novel conceptual approaches. A second aim, therefore, is to highlight contemporary efforts to (1) integrate evolutionary and developmental neurobiology, (2) animate the subject of comparative neuroanatomy by linking it to physiology and behavior, and (3) use comparative analyses to discover general rules about how neural systems function and change.

A BRIEF HISTORY OF SCIENTIFIC PROGRESS IN COMPARATIVE NEUROBIOLOGY

Early theories of brain evolution were dominated by the idea that brain size and complexity increased steadily over evolutionary time. Although it was acknowledged that brains do not fossilize, a phylogenetic increase in brain size and complexity seemed evident to the early theorists when they compared animals occupying successive rungs of the so-called phylogenetic scale. Thus, brain size (relative to body weight) and complexity (degree of differentiation) were seen to increase in a roughly linear manner from fish to amphibians, reptiles, birds, primitive mammals, primates, and finally humans. This steady increase in brain complexity was viewed as having occurred primarily by the sequential addition of new parts to the existing ancestral brains. That the linear and additive view of brain evolution remains influential to the present day is evident from the still widely accepted usage of terms such as infrahuman primates, submammalian vertebrates, paleocortex, and neocortex.

The best example of the linear and additive view of brain evolution is the still popular theory that the forebrain (the most anterior portion of the brain) steadily increased in both size and complexity as evolution proceeded from fish to man. According to this view, the forebrain in primitive vertebrates, such as fishes and amphibians, was considered to be small, relatively undifferentiated, and dominated by the sense of smell. With the origin of reptiles and birds, the forebrain was thought to have increased in size and to have evolved a new region, termed the primordial neopallium, which supposedly processes primarily nonolfactory sensory information. A true neocortex (differing from the primordial neopallium primarily in having a highly layered structure) was thought to have evolved only in mammals, reaching its greatest size and complexity in humans. According to this view, reptiles and birds exhibit primarily stereotyped instinctive behaviors because their forebrains consist primarily of striatal (noncortical) structures, while mammals exhibit behavioral plasticity and learning because they possess a true neocortex.[1,2]

Despite its still widespread appeal, this old theory of forebrain evolution has been largely discredited by subsequent research. With regard to behavior, a large body of research now shows that reptiles and birds may exhibit very complicated forms of learning and behavioral plasticity.[3] With regard to brain anatomy, novel techniques developed in the 1950s to study the chemical composition and axonal connections of brain structures revealed several errors made by early investigators in their interpretation of forebrain structures. Most importantly, these new methods have proven that (1) olfactory inputs to the forebrain in fishes and amphibians are far more restricted than previously believed and (2) the striatal (noncortical) structures of the forebrain in reptiles and birds are far smaller than previous investigators had assumed. Collectively, these findings demonstrated that the neocortex is not really new in mammals but that something like it appeared quite early in vertebrate evolution.[4] More generally, these findings caused most comparative neurobiologists to abandon the linear and additive view of brain evolution, proposing instead that the fundamental divisions of the brain are present in all vertebrates and that brains evolve primarily by modifying these basic divisions. This new paradigm initiated an extensive and ongoing search for the conserved (i.e., homologous) brain regions in all of the major vertebrate groups.

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Although the identification of conserved brain regions among vertebrates has been largely successful, instances of apparent nonconservation did create significant problems for the field. These problems arise from the fact that features which appear in only a subset of vertebrates could have (1) been invented in only one branch of the evolutionary tree, (2) been lost in one or more lineages, or (3) evolved several times independently in different lineages. But how is one to discriminate between these hypotheses? Moreover, the existence of evolutionary change is obvious from the fact that even conserved features often differ in many minor aspects between species, but how is one to determine the directionality of such changes? Early theorists such as Herrick had generally interpreted simpler features to be more primitive, but comparative neurobiologists in the second half of the century were no longer so certain that evolution always proceeds from simple to complex. It also became increasingly untenable to say that primitive features are those that are found in animals low on the phylogenetic scale, because the logic of Darwin's argument dictates that evolution produces phylogenetic trees and bushes, not scales and ladders. Finally, even if one knew that a group of organisms branched off early from the phylogenetic tree, one could still not be certain that all of their features are primitive, because even so-called primitive organisms certainly possess at least some derived (not primitive) features. Faced with these difficulties, comparative neurobiology threatened to deteriorate into the mere gathering of facts about species similarities and differences that could not be linked to scenarios of evolutionary change by anything other than reckless speculation.

At this point, comparative neurobiology was aided by revolutionary developments in the field of taxonomy, in which Willi Hennig[5] and others formalized a logically rigorous method, called cladistics, for reconstructing phylogenetic trees. In essence, cladistics relies on the analysis of many features to determine which of the many possible phylogenetic trees entails the smallest number of independent evolutionary changes. Assuming that the evolutionary process is conservative (i.e., that features are more likely to have evolved once than to have evolved multiple times independently), cladistics reveals the true phylogenetic tree, provided a sufficiently large number of features have been analyzed. This methodology revolutionized the field of taxonomy primarily because it permitted the falsification of previously established phylogenetic trees by showing that the available data were more consistent with alternative trees. Taxonomists have used this new methodology, and a plethora of new data about molecular similarities and differences between species, to establish increasingly robust phylogenetic trees. These improved trees could then be used by comparative neurobiologists to answer questions about the evolutionary history of individual neural features. Most importantly, the distribution of a particular neural feature on the phylogenetic tree reveals whether this feature is more likely to have evolved just once or several times independently. In the former case, the feature would be considered homologous across the species, while in the latter case the features would be similar but nonhomologous (e.g. due to convergent evolution). In addition, comparative neurobiologists could use cladistic methods to determine which characters were most likely to be primitive (and which derived) and thus to determine the likely directionality of evolutionary change.[6,7]

The most important finding to emerge from the application of cladistic methods to the study of brain evolution was that brain size and complexity increased several times independently among vertebrates, namely within the bony fishes, sharks, birds, cetaceans, and primates. Coral reef fishes, parrots, and dolphins, for example, all have large and complex brains not because they are near the top of an overall phylogenetic scale but because they are all members of taxonomic groups in which there has been a local trend towards increasing brain size and complexity. Moreover, neurocladistic analyses revealed that in some lineages, such as lungfishes and amphibians, brains have actually decreased in both size and complexity. One important implication of this discovery was that salamander brains are secondarily simplified and cannot be representative of the ancestral vertebrate brains as Herrick had assumed. More generally, the cladistic analyses of brain evolution proved beyond any reasonable doubt that vertebrate brains evolved not in any simple linear manner from simple to complex but in a number of divergent directions in different lineages.

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Although new methodologies, new techniques, and additional data thus effectively debunked most of the once cherished theories about brain evolution, news of this scientific progress seems not to have traveled far beyond the ranks of practicing comparative neurobiologists, for the same old theories about brain evolution are still espoused by an alarming number of neuroscientists. One important reason for this lack of general influence is that the new discoveries of comparative neurobiology were never adequately summarized for a wider audience. This situation has now been rectified with the recent publication of two scholarly books on the progress in comparative neurobiology.[8,9] Although these books will certainly help to disseminate the modern views on brain evolution, the field of comparative neurobiology continues to face several challenges which must be addressed if it is to become more widely influential within the mainstream of neuroscience. These challenges include (1) how to integrate comparative neurobiology with genetics and embryology, (2) how to link evolutionary changes in anatomy to physiology and behavior, and (3) how to expand the field beyond the reconstruction of history into the realm of general rules, laws, and theories. These issues are addressed below.

THE RELATION OF BRAIN DEVELOPMENT TO BRAIN EVOLUTION

The notion that developmental data can be used to test phylogenetic hypotheses has long been entertained by comparative biologists. Shortly after Darwin published his *Origin of Species*, the German biologist and philosopher Ernst Haeckel argued that ontogeny recapitulates phylogeny and that evolutionary biologists needed simply to examine an organism's developmental history to discover its phylogenetic history. Unfortunately, however, Haeckel's famous dictum has also been amply disproven, for organisms in their development do not always or even generally repeat the adult forms of their ancestors. The kind of recapitulation envisioned by Haeckel occurs only if ancestral ontogenies change during evolution in such a manner that they become extended beyond their normal end point (i.e., the ancestral adult). This does happen sometimes, but in many cases evolution modifies ancestral ontogenies before they reach their normative end point by deflecting them into alternate developmental trajectories and towards divergent ends. In these cases, ancestral and descendant ontogenies share only embryonic stages, not any adult forms, and multiple descendant ontogenies resemble each other only up to a point, after which they diverge. The demise of Haeckelian recapitulation as a general law has therefore given rise to a more modern view of phylogenetic transformation as developmental divergence.

This modern view of the relation between ontogeny and phylogeny can

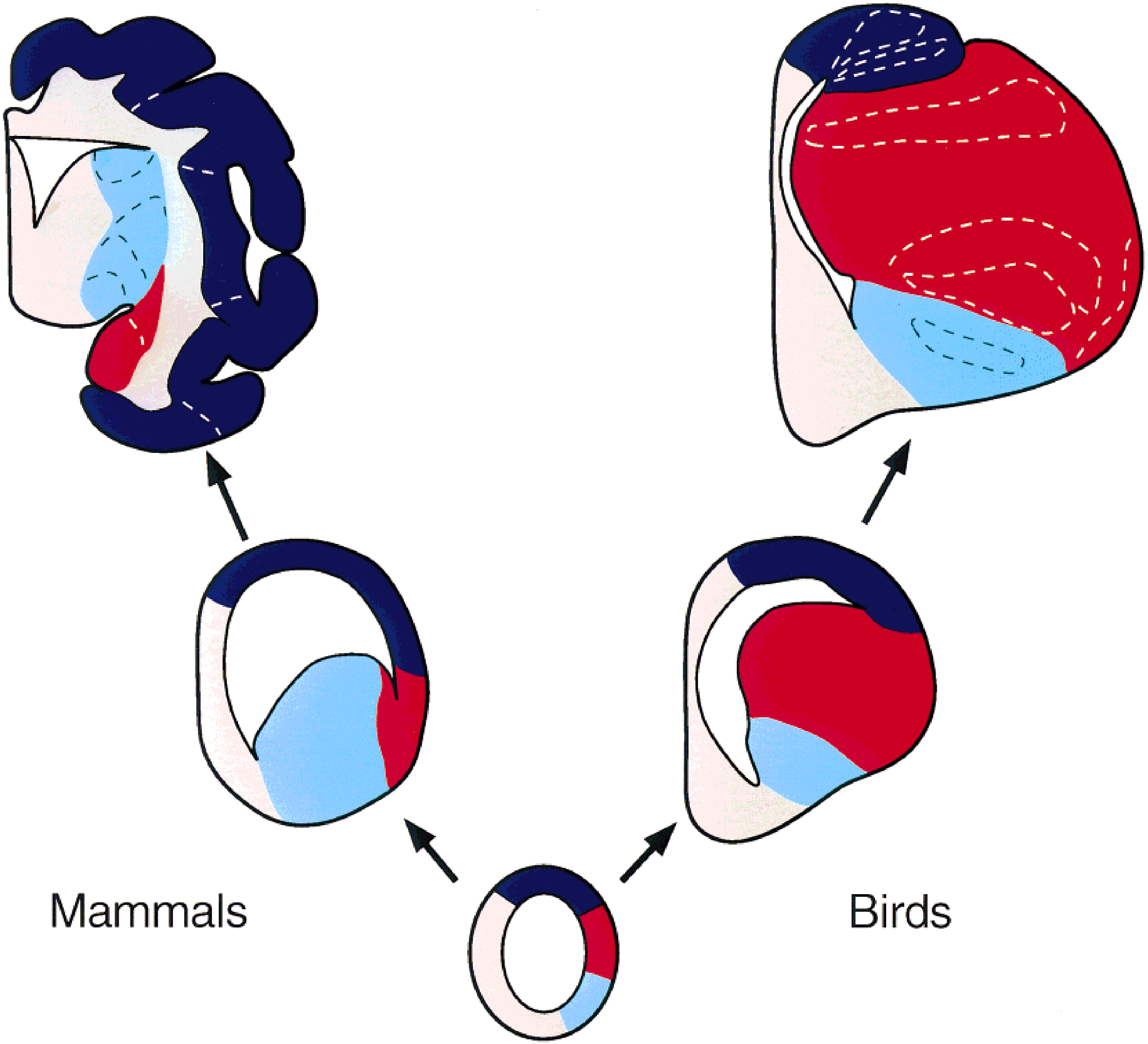

Fig. 1. Schematic illustration of how the telencephala of birds and mammals are similar in early development but then diverge such that their adult subdivisions are difficult if not impossible to homologize. Dorsal (dark blue), lateral (red), and ventral (light blue) zones in the embryonic telencephalon are indicated. The ventral and dorsal zones become very large and well differentiated in mammals, whereas the lateral zone develops into a large and complex structure in adult birds.

illuminate and largely resolve numerous long-standing disputes about the homology of adult structures that differ dramatically from one another. Homologies of adult structures in the forebrain of birds and mammals, for example, have been debated for nearly 100 years.[10] Many of these hypotheses remain unresolved, primarily because the telencephalon (the most anterior and dorsal portion of the forebrain) is so different in adult birds and mammals that many structures in one group cannot readily be identified in the other (Fig. 1). Different investigators have therefore championed different hypotheses of homology between different adult structures and have adduced different kinds of data to support their claims. From there, the debate has tended to degenerate into arguments about which kind of data are most valuable in establishing hypotheses of homology. Thus, some investigators have claimed that similarity in neural connections is the most valuable criterion of homology,[11] while others have favored similarities in relative position, cytoarchitecture, developmental origin, neurotransmitter content, or patterns of gene expression. The fundamental problem with this debate, however, is that the evolutionary process can, in principle, change any aspect of a feature without negating its homology across species. Even patterns of gene expression can and do change during the course of evolution. Therefore, no single kind of similarity data can a priori be considered more valuable than any other.[7] If many kinds of similarity data all support the same hypothesis of homology, then that hypothesis can be established as superior to the alternative hypotheses, but if the features being compared have diverged dramatically in adult structure, as is the case for the telencephalon in birds and mammals, then different kinds of similarity data may support different hypotheses of homology, and interminable debate seems inevitable.

Such protracted disputes undermine the claim of comparative neurobiologists that their hypotheses have become increasingly testable, but they can be largely avoided if the problem is reconceptualized as a comparison between entire ontogenies rather than exclusively adult structures. Application of this comparative embryological approach to the problem of telencephalic evolution reveals that avian and mammalian telencephala resemble each other closely in the early embryonic stages and diverge only later in development (Fig. 1). A reasonable strategy for studying telencephalic evolution, therefore, is to begin with a search for conserved embryonic features and then to ask how the subsequent development of these embryonic features has diverged between species.

Although the data required for such a comparative analysis of telencephalic development are still rather fragmentary, recent studies have shed some light on this problem, and a tentative model of telencephalic development and evolution can already be constructed.[12] According to this model, the telencephalon of both birds and mammals begins as a thin-walled outpocketing at the front of the brain. Soon after this early evagination, the embryonic telencephalon becomes divided into several compartments, or zones, which are likely to be conserved among birds and mammals.[8,13] The later development of these early compartments diverges between birds and mammals, particularly in the lateral region of the telencephalon, which is divisible into ventral, lateral, and dorsal zones (Fig. 1; light blue, red, and dark blue, respectively). Most strikingly, in mammals the ventral and dorsal zones thicken dramatically, whereas in birds the lateral zone attains gargantuan proportions. If the development of these zones differed only in relative size, then comparisons between adult structures would present no special problems. However, as the different embryonic zones grow differentially in the different species, they also become parceled into different numbers (and kinds) of subdivisions. Whenever there are such mismatches in the number of subdivisions, some of the adult subdivisions in one species must lack a homolog in the other. Therefore, although the embryonic telencephalic zones may be homologous between birds and mammals, many of the adult telencephalic structures in both birds and mammals are the result of such divergent development that they must be considered genuinely new.[14]

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This example suggests that when adult homologies are debated endlessly, they probably don't exist. Ever since comparative neurobiologists toppled the old theory of linear evolution by sequential addition of new structures, they have been guided by the assumption that adult neural structures should be generally conserved across vertebrates. But perhaps this assumption is incorrect for cases in which there has been a significant amount of developmental divergence. In such cases, perhaps, comparative neurobiologists should search for homologs also among embryonic brains, where one can expect more phylogenetic conservation. Having found conserved embryonic features, comparative neurobiologists should then focus on exactly how the subsequent development diverges between species. Specifically, they might ask what cellular and molecular changes are responsible for diverting ontogenetic trajectories down one route or another. Although we are far from being able to answer this question for the case of telencephalic evolution, such questions are in principle addressable with the techniques of classical embryology and developmental genetics. As these techniques are applied to questions of developmental divergence over evolutionary time, comparative neurobiologists will probably forget about some of their old debates and develop new hypotheses about phylogenetic transformations that are framed in terms of genetic changes and developmental mechanisms. The prospect of someday testing phylogenetic hypotheses at the level of developmental mechanisms is bound to inspire future generations of comparative neurobiologists.

INTEGRATING STRUCTURAL BRAIN EVOLUTION WITH PHYSIOLOGY AND BEHAVIOR

Textbooks of comparative neurobiology tend to be rather lengthy treatises, filled with exhaustive neuroanatomical descriptions and reconstructions of structural brain evolution, but they rarely say much about how structural brain evolution is related to brain physiology or animal behavior. The few prior attempts to link structural changes to changes in function generally take the form of correlations between the size and complexity of a particular brain region and the organism's known behavioral abilities. For example, the observation that birds have relatively poorly developed olfactory bulbs is correlated with the behavioral observation that most birds have a relatively poor sense of smell. Similarly, the large size of the gustatory lobes in the brainstem of goldfishes is correlated with their highly developed sense of taste. These correlations are relatively easy to establish because olfactory bulbs and gustatory lobes are so clearly connected to their respective sensory modalities. For most neural structures, however, functional roles are more difficult to fathom. Fortunately, technological developments have provided us with a whole battery of methods, such as functional brain imaging and neurophysiological recording, to derive hypotheses about the behavioral function of neural structures. These can then be used to postulate causal links between anatomical species differences and behavioral evolution. For instance, a wide variety of data have implicated the prefrontal cortex in the planning of actions and anticipation of consequences, and these data support the hypothesis that the large size of the prefrontal cortex in humans is at least partly responsible for our highly developed ability to think ahead.

Unfortunately, however, this approach is severely limited because we already know that most if not all brain regions function in multiple behaviors and that any one behavior depends not on single brain structures but on entire circuits of interconnected neurons. This observation undermines the basic premise that straightforward correlations between anatomical variation and behavioral differences should exist and explains why previous attempts to find such correlations tended to remain rather vague (and uninspiring). In fact, the realization that all behaviors are controlled by circuits perforce shifts one's attention away from the phylogeny of single structures and toward the phylogeny of neural circuits. To actually study the evolution of neural circuits is not a simple proposition, however, because neural circuits are difficult to delimit from each other and may function in several distinct behaviors. Progress can, however, be made by examining specific neural circuits in which these problems are minimized. Such a circuit is the vocal control system in songbirds.

Songbirds (e.g., finches and sparrows) are named for their remarkable ability to sing complex songs, which they typically learn from other birds. This ability to sing and learn songs is controlled by an interconnected array of brain regions, called the song system, which has only sparse connections with other brain regions and functions primarily in vocal control.[15] Because the song system is so well circumscribed in terms of both connections and behavioral function, one can ask how this circuit has changed over evolutionary time. Specifically, one can ask whether a homologous vocal control circuit exists in birds such as chickens, which do not learn their vocalizations but instead develop them without having to hear other birds. Research into this question has revealed that birds which do not learn their songs (henceforth called nonlearners) possess brainstem and midbrain vocal control regions that are homologous to those in songbirds but that they apparently do not involve their forebrain in the control of vocalization.[16] This suggests that the vocal control circuit expanded during the evolution of songbirds to incorporate several forebrain elements that were not hitherto part of the vocal control circuit. Since the forebrain is generally associated with complex behaviors and behavioral plasticity, the evolutionary cooption of forebrain elements into the vocal control circuit may have been one critical factor in letting songbirds evolve their ability to learn complex songs.

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The finding that nonlearners possess no forebrain vocal control regions raises the question of how songbirds evolved the forebrain components of their song system. According to one hypothesis, songbirds evolved these regions de novo, without apparent homologues in nonlearners. This hypothesis is supported by the apparent absence of indisputable homologues for most of the forebrain song nuclei in nonlearners. The de novo hypothesis is limited in its usefulness, however, because it is based entirely on comparisons between adult structures and therefore cannot address the related question of how songbirds modified their ancestral developmental pathways to create the song system.

An alternative hypothesis, based on the realization that phylogenetic transformation is developmental divergence, might state that some forebrain regions in songbirds were developmentally modified (during evolution) in such a way that they became connected to the midbrain and medullary vocal control regions. According to this hypothesis, songbirds and nonlearners might possess homologous forebrain regions, at least during early development, but only songbirds sprout connections from these regions to the lower vocal control centers. Although some data are consistent with this second hypothesis, these ideas remain speculative because too little is currently known about the vocal control system in nonlearners or about the development of the vocal control system in any bird. Ultimately, however, it seems likely that a comparative developmental approach of this kind will be required to understand how evolutionary changes at the level of individual neurons, brain regions, and neural circuits are related to the evolutionary emergence of new behaviors, such as the ability of songbirds to learn their songs.

THE QUESTION OF HUMAN RELEVANCE: WHY STUDY BRAIN EVOLUTION?

But why should we care what evolutionary changes enabled songbirds to learn their songs or how forebrain development diverges between birds and mammals? In these days of limited research budgets and renewed opposition to evolutionary biology from religious quarters, why invest time and resources to study nonhuman brains? In the past, scientists who studied the brains of birds, fishes, frogs, and invertebrates often justified their research by claiming that these systems should be simpler to understand than the human brain and that discoveries made in these simple systems would be applicable also to complex systems. This simple systems approach lost much of its force, however, when comparative biologists realized that even the "lower" animals, such as invertebrates, often possess remarkably complex nervous systems. Moreover, the complexity seen in different animal groups is often the result of divergent evolution, and understanding one complex system therefore does not necessarily contribute very much to the understanding of other complex systems. For example, why should one study the neural mechanisms of motor pattern generation in invertebrates if the data suggest that rhythmic motor patterns are generated by a broad variety of mechanisms in different animal groups?[17]

As an alternative to the simple systems approach, one may argue that many nonhuman systems, particularly those in invertebrates, present certain practical advantages that make them easier to study. The large size of the giant axons in squids, for example, enabled researchers to insert microelectrodes into axons and discover the ionic basis of the action potential. Discoveries made in squid giant axons were then found to hold generally true also for other axons in other animal groups. A similar rationale underlies all attempts to use nonhuman organisms as model systems to find general rules and regularities that are applicable also to humans. Although this model systems approach has been extremely successful with regard to the fundamental cellular and molecular mechanisms of nervous system function, it is more difficult to apply as one considers more complex phenomena, such as motor pattern generation.[17] In general, it appears that the generality of biological laws decreases as the complexity of the phenomena which they describe increases. Therefore, if one's goal is to understand complex phenomena occurring in the human brain, then one should choose model systems that are closely related to humans (e.g. other primates). Even if one picks closely related model species, however, phylogenetic conservation can never be taken for granted, because either the model species or humans may have changed some aspect of the phenomenon during the course of their own evolutionary history. The concept of homology therefore lies at the heart of the model systems approach, and the validity of a model must always be confirmed by studies directly on humans.

Although both the simple and the model system approaches are thus founded on the belief that findings in one system will generalize to another, both approaches are limited by the tendency of evolution to induce change and undermine the universality of biological laws (at least for the relatively complex phenomena found in the nervous system). This limitation has induced some authors to despair of finding regularities in the evolutionary process and to conclude that evolutionary biology is merely the reconstruction of history, devoid of any explanatory power.[18] This conclusion is overly pessimistic, however, because evolutionary change is not completely haphazard. Evolution must change what already exists, and ancestral history therefore influences the course of subsequent evolution. Knowledge of this history can help enormously in explaining why a structure functions the way it does, particularly in cases where its design seems counterintuitive from a human engineering perspective. In addition, the evolutionary process is constrained by the general rules of what constitutes a viable organism. Bilateral symmetry, for example, seems to be a vital aspect of all vertebrate organisms, and no vertebrates have evolved wheels that rotate about an axle. Biology may lack universal laws akin to those of Newton, but it abounds with rules or constraints that may have their exceptions but are sufficiently general to convince us that nature is not entirely ruled by chance. And the comparative method is the most powerful tool available for the discovery of such general biological constraints.

Although the details of how songbirds and parrots learn their vocalizations may differ from each other or from how humans learn language, the vocal abilities of all three animal groups evolved within a common framework of constraints.

To this end, the comparison of biological systems that have independently evolved similar features in response to similar biological problems is particularly useful. For example, the observation that dolphins and sharks have convergently evolved similar body shapes has long been used to support and construct arguments about how vertebrate bodies should be constructed to maximize hydrodynamic efficiency. Similarly, the observation that songbirds and parrots have independently evolved vocal learning and have both evolved vocal control circuits that include forebrain components supports the hypothesis that the forebrain must be involved if a system is to be capable of vocal learning. The latter hypothesis is further supported by the finding that humans (i.e., the third major group to have independently evolved vocal learning) have also evolved vocal control circuits that include numerous forebrain components.[19] Thus, although the details of how songbirds and parrots learn their vocalizations may differ from each other or from how humans learn language, the vocal abilities of all three animal groups evolved within a common framework of constraints. Knowledge of these constraints can be used to guide research on humans and will help us to understand why the human system is organized the way it is. Ultimately, therefore, a complete understanding of the human brain will require that we know which of its many features are due to general biological constraints, which represent uniquely human innovations, and which are holdovers from ancestral brains. This knowledge can be attained only by a comparative analysis of many nonhuman brains.

CONCLUSIONS

When Darwin announced that humans descended from nonhuman ancestors, he initiated an enormous amount of research into how humans are different from other animals and how they are the same. The earliest theories of brain evolution were grand but speculative, based as they were on the presumption that brains evolved in a linear manner from fish to man. These early views have now been disproven by new data and, more importantly, by more rigorous methods of testing phylogenetic hypotheses. As comparative neurobiology thus emancipated itself from the speculative realm, its ambitious theories and general laws were replaced by numerous detailed accounts of how particular brain structures evolved in the various animal groups. The empirical and theoretical grounding of comparative neurobiology therefore came at a cost to its scope and generality. This trend can now be reversed, however, as comparative neurobiology stands at the brink of being integrated with developmental neurobiology and genetics, is increasingly able to address how evolutionary changes in brain anatomy influence behavior, and can be used to derive general rules about how brains change during evolution to solve specific biological problems.

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