Evolutionary Convergence in Nervous Systems: Insights from Comparative Phylogenetic Studies

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Key Words

Animal behavior · Electric fish · Electric communication · Frogs · Neuroethology · Owls · Phylogeny · Prey capture · Sound localization

Abstract

Over the past 20 years, cladistic analyses have revolutionized our understanding of brain evolution by demonstrating that many structures, some of which had previously been assumed to be homologous, have evolved many times independently. These and other studies demonstrate that evolutionary convergence in brain anatomy and function is widespread. Although there are relatively few neuroethological studies in which brain and behavior have be studied within an evolutionary framework, three relatively well studied cases are reviewed here: electric communication among gymnotiform and mormyriform fishes, prey capture among frogs, and sound localization among owls. These three examples reveal similar patterns of brain evolution. First, it is clear that novel abilities have evolved many times independently in taxa whose common ancestors lack these abilities. Second, it is apparent that small changes in neural pathways can lead to dramatic changes in an organism's abilities. Brain evolution at this small scale is quite common. The behavioral importance of small scale changes on one hand, and the pervasiveness of convergent evolution on the other, have several implications for understanding brain evolution. First, similar abilities may be conferred by convergent rather than homologous circuits, even among closely related species. Furthermore, closely related species may use the same information in different ways, or they may use different means to obtain the same information. One reason that convergence is so common in the biological world may be that the evolutionary appearance of novel functions is associated with constraints, for example in the algorithms used for a given neural computation. Convergence in functional organization may thus reveal basic design features of neural circuits in species that possess unique evolutionary histories but use similar algorithms to solve basic computational problems.

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Introduction

Over the last 20 years, cladistic studies have revolutionized our understanding of brain evolution by demonstrating that many structures, previously assumed to be homologous, in fact have evolved many times indepen-

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dently [Northcutt, 1984; Nishikawa, 1997]. The most clear-cut examples of convergent evolution involve the appearance of similar features with similar functions in distantly related taxa whose common ancestor lacked the feature. Examples are many, including the evolution of color vision in bees and primates [Pichaud et al., 1999]; the olfactory glomeruli of neopteran insects and vertebrates, which share an impressively detailed suite of morphological and physiological similarities [Strausfeld and Hildebrand, 1999; Eisthen, 2002]; the evolution of electric organs and electric communication in gymnotiform and mormyriform fishes [Bullock et al., 1975; Kawasaki, 1993]; the evolution of a variety of cerebellum-like structures among vertebrates [Bell, 2002]; expansion of the hippocampus in food-storing corvid [Basil et al., 1996] and parid [Healy and Krebs, 1993] birds; hypoglossal afferents in the tongues of frogs [Nishikawa, 1999], birds [Wild, 1990] and mammals [Lowe, 1981]; the evolution of song learning in oscine birds and parrots [Nottebohm, 1972; Striedter, 1994]; and the evolution of divisions of the mammalian sensory isocortex, such as area MT in primates and carnivores [Northcutt and Kaas, 1995; Kaas, 2002]. More enigmatic are cases in which a feature appears repeatedly and independently within a relatively restricted taxonomic group. An intriguing example is the case of asymmetrical ears which, during 580 million years of vertebrate evolution, appeared only in owls. Among owls, however, asymmetrical ears evolved at least four and perhaps as many as seven times independently [Norberg, 1977; Volman and Konishi, 1990].

There are numerous cases in which convergent evolution is suspected, but for which definitive information on the presence or absence of the character in the common ancestor is lacking. One example is the auditory neurons of birds and mammals that are responsible for time-coding, which also share an impressive suite of specialized membrane and synaptic properties for coincidence detection [Carr et al., 2001; Carr and Soares, 2002].

It is important to note that, although not contradicting an hypothesis of homology, neither similarity of structure, nor even similarity of developmental regulatory genes [Harris, 1997; Wray, 2002], alone constitutes sufficient evidence for rejecting an hypothesis of convergent evolution. The character in question must also be present in the common ancestor. In contrast, either dissimilarity of structure or absence of the character in the common ancestor is sufficient to reject an hypothesis of homology.

As for most characteristics of organisms, from morphology to molecules [see Zakon, 2002], the evolutionary history of brains as well as the behavior they produce appears to be characterized by pervasive convergent evolution. The frequent occurrence of convergence during brain evolution is due to two factors: high rates of evolution in general [Nishikawa, 1997; Katz and Harris-Warrick, 1999]; and the existence of common selective pressures imposed by fundamental biophysical constraints which, over time, have produced similar neural networks for performing similar computations.

In the vertebrate brain, relatively few major new structures have appeared during more than 580 million years of evolution [Nishikawa, 1997]. Likewise, in invertebrates, identified neurons and the circuits they comprise appear to be highly conservative within and even between phyla [Edwards and Palka, 1991; Katz and Harris-Warrick, 1999]. Nevertheless, small changes in neural circuits are common and can lead to profound differences in function [Nishikawa, 1997; Katz and Harris-Warrick, 1999].

At first glance, evolutionary convergence may appear to complicate evolutionary studies of the nervous system by confounding efforts to identify homologous structures. Upon reflection, however, it is clear that convergent evolution can be an important tool for neuroscience, primarily by revealing basic design features of neural systems. Examples include algorithms used by mormyrid and gymnotid fishes for determining the sign of the difference in phase between a fish's own electric organ discharge and a jamming stimulus from another fish [Kawasaki, 1993; Carr and Friedman, 1999] and time coding circuits in birds and mammals [Carr et al., 2001; Carr and Soares, 2002].

The goal of this paper is to review three case studies for which comparative phylogenetic studies have demonstrated convergent evolution of neural substrates and behavior: 1) the evolution of electric organs and electric communication in gymnotiform and mormyriform fishes; 2) the evolution of proprioceptive afferents that modulate prey capture in frogs; and 3) the evolution of asymmetrical ears and sound localization among owls. For each example, the behavior and its neural control are briefly reviewed, a cladogram is given to illustrate the evolution of the behavior within the group, and the evolutionary patterns and general conclusions are discussed.

Electric Organs and Electric Communication in Gymnotiform and Mormyriform Fishes

Weakly electric fishes live in turbid water and possess specialized electric organs that generate electric signals, as well as an electrosensory system that perceives them [Bul-

lock and Heiligenberg, 1986]. Electric signals are used in social communication and to locate stationary and moving objects in the environment. Social signals are used in agonistic and courtship displays, and may provide information about the species, sex, size, maturation, location, distance and individual identity of the sender. Behavioral repertoires include echoes, duets, and other complex interactions [Hopkins, 1988].

Two different types of discharge patterns are produced by electric organs. The wave-type electric organ discharge (EOD) is quasi-sinusoidal, occurs at a constant rate, and is characterized by a frequency spectrum with narrow peaks at the fundamental frequency and the higher harmonics [Bullock, 1970]. Pulse-type discharges are separated by relatively long intervals and have a broader frequency spectrum [Heiligenberg, 1977].

When two wave-type fishes with similar EOD frequencies encounter each other, their electric fields interfere and their ability to electrolocate or communicate deteriorates. To avoid mutual jamming, fish shift their discharge frequencies away from each other to create a larger frequency difference [Bullock et al., 1972]. In *Eigenmannia*, the frequency shift is always in the direction that immediately reduces frequency overlap. Thus, to implement the jamming avoidance response, a fish must be able to detect the direction of the difference in phase between its own signal and that of its neighbor [Rose et al., 1987].

Electric organs evolved independently (fig. 1) in South American knifefishes (Gymnotiformes, Ostariophysi) and African elephantfishes (Mormyriformes, Osteoglossomorpha) [Alves-Gomes et al., 1995; Alves-Gomes, 1999]. Due in large part to their importance in neuroethology, molecular phylogenies are available for both Gymnotiformes [Alves-Gomes et al. 1995; Alves-Gomes, 1999] and Mormyriformes [Sullivan et al., 2000]. Despite its independent origin in mormyriform and gymnotiform fishes, many aspects of electric communication are strikingly similar in the two groups, including the production of wave-type EODs and a jamming avoidance response. A wave-type EOD appears to have evolved in the common ancestor of mormyriforms [Sullivan et al., 2000] and is present in the basal taxon Gymnarchus [Kawasaki, 1993]. Within gymnotiforms, a wave-type EOD appears to have evolved independently in *Sternopygus* and in the common ancestor of *Eigenmannia* and *Apteronotus* (fig. 1) [Alves-Gomes et al., 1995].

Like the wave-type EOD, a jamming avoidance response also evolved independently in *Gymnarchus* and *Eigenmannia* and, despite differences in neural substrates, they use the same algorithm to calculate the direc-

tion of the difference in phase between the fish's own signal and a neighboring signal [Kawasaki, 1993]. Both taxa use electrosensory organs to detect the mixture of the fish's own reafferent signal and the exafferent signal, the time course of amplitude and phase modulation is analyzed at each area of the body surface, detection of phase modulation occurs by comparing the phase of the two signals at different areas on the body, and ambiguity is reduced by integrating across all body areas. In *Eigenmannia*, phase comparisons take place in the midbrain torus semicircularis, whereas they take place in the electrosensory lateral line lobe of the medulla in *Gymnarchus* [Kawasaki, 1993].

Even within gymnotiforms, there are interesting similarities and differences among closely related species in the neural circuits that control jamming avoidance. First, although *Sternopygus* lacks a jamming avoidance response (fig. 1), it nevertheless possesses midbrain neurons that can discriminate the direction of the difference in phase between the fish's own signal and an interfering signal, suggesting that the circuitry used for jamming avoidance in *Eigenmannia* and *Apteronotus* may have been co-opted from more general-purpose circuitry that *Sternopygus* uses for detection of moving objects and conspecifics in its environment [Rose et al., 1987]. Second, although both *Eigenmannia* and *Apteronotus* (fig. 1) exhibit a jamming avoidance response and similar premotor circuits [Heiligenberg et al., 1996], there are interesting differences in control of the jamming avoidance response between species. In both *Eigenmannia* and *Apteronotus*, a jamming stimulus that is below the fish's own frequency causes individuals of both species to increase their EOD frequency. In contrast, if the jamming stimulus is above the fish's own frequency, *Eigenmannia* will decrease its frequency, but *Apteronotus* will increase it even more. To increase EOD frequency, *Eigenmannia* recruits the diencephalic prepacemaker nucleus, whereas to decrease EOD frequency, the sublemniscal prepacemaker nucleus is inhibited [Metzner, 1993]. *Apteronotus* possesses both pathways, but uses only the diencephalic prepacemaker nucleus to modulate its EOD frequency. In *Apteronotus*, lesions of the sublemniscal prepacemaker nucleus have no effect on the jamming avoidance response [Heiligenberg et al., 1996].

Both wave-type EODs and jamming avoidance responses have evolved convergently in mormyriform and gymnotiform fishes. The similarity in the algorithms used to compute the direction of phase difference between a fish's own and an interfering signal, despite differences in the neural substrates where the calculations are per-

Fig. 1. Cladogram illustrating convergent evolution of wave-type electric organ discharge (EOD) and jamming avoidance responses in African mormyrid and South American gymnotid fishes [based on Alves-Gomes et al., 1995]. The common ancestor of mormyrids and gymnotids was non-electrogenic. Wave-type EODs and jamming avoidance responses evolved independently in *Gymnarchus* and in the common ancestor of *Eigenmannia* and *Apteronotus. Sternopygus* possesses a wave-type EOD but lacks a jamming avoidance response.
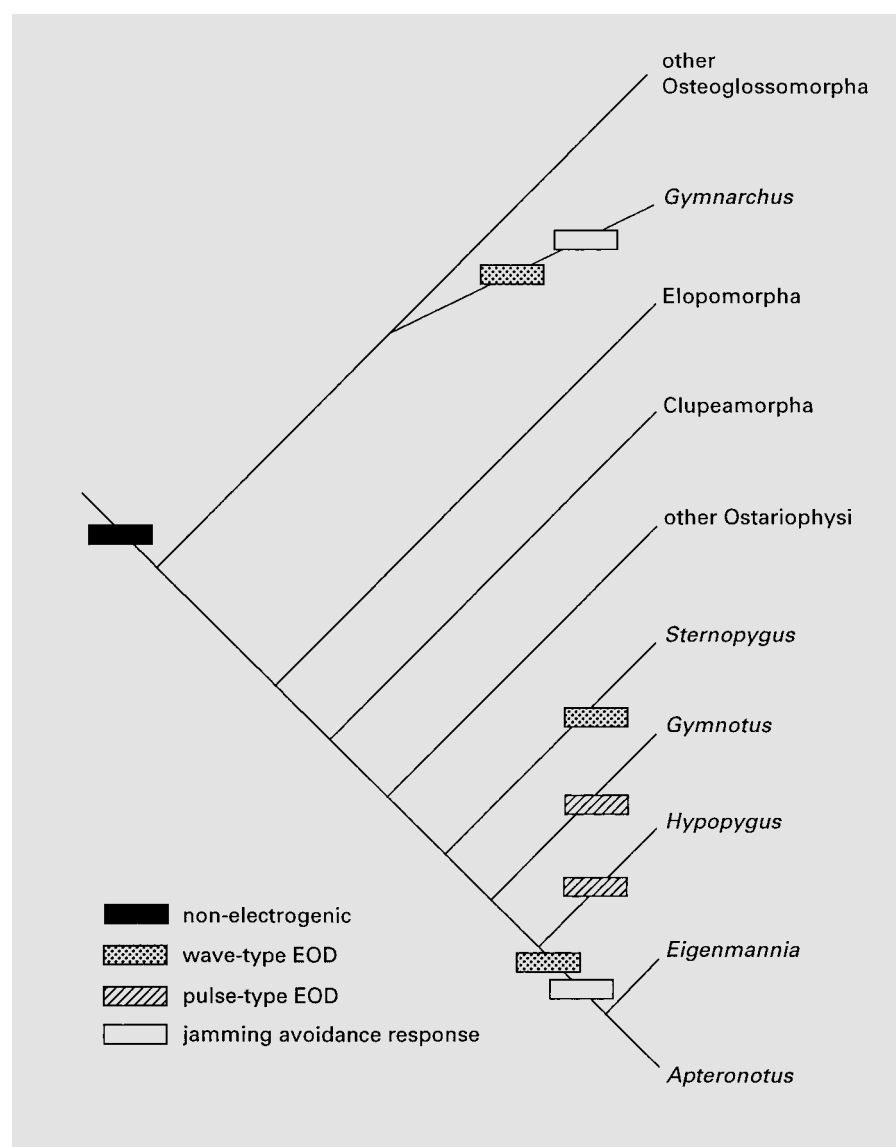
formed, suggests that common selective pressures imposed by fundamental biophysical constraints have produced similar neural networks in the hindbrain of mormyrids and the midbrain of gymnotids for performing this computation. The diversity in behavior and modulation of EOD frequency within closely related gymnotiform species also suggests that relatively small changes in existing pathways can lead to larger changes in behavior, and that similar circuits may be present, but are nevertheless used for different purposes, in closely related species [Nishikawa, 1997; Katz and Harris-Warrick, 1999; Metzner, 1999].

Prey Capture in Frogs

All frogs possess relatively simple tongues that contain only two pairs of muscles, which protract and retract the tongue during prey capture [Mallett et al., 2001]. Three different mechanisms for protracting the tongue (mechanical pulling, inertial elongation, and hydrostatic elongation) have evolved among frogs. Each is characterized by different biomechanical properties and different mechanisms of neuromuscular control [Nishikawa, 1999]. Frogs primitively possess short tongues that are protracted by mechanical pulling (fig. 2). In mechanical pullers, the tongue shortens to ~60–70% of resting length during pro-

Fig. 2. Cladogram illustrating convergent evolution of ballistic tongue projection (via inertial elongation) and hypoglossal afferents among anurans [based on Ford and Cannatella, 1993; Nishikawa, 1999]. The common ancestor of anurans used mechanical pulling to protract its tongue and lacked hypoglossal afferents. Inertial elongation and hypoglossal afferents that modulate jaw muscle coactivation evolved up to five times independently among anurans.
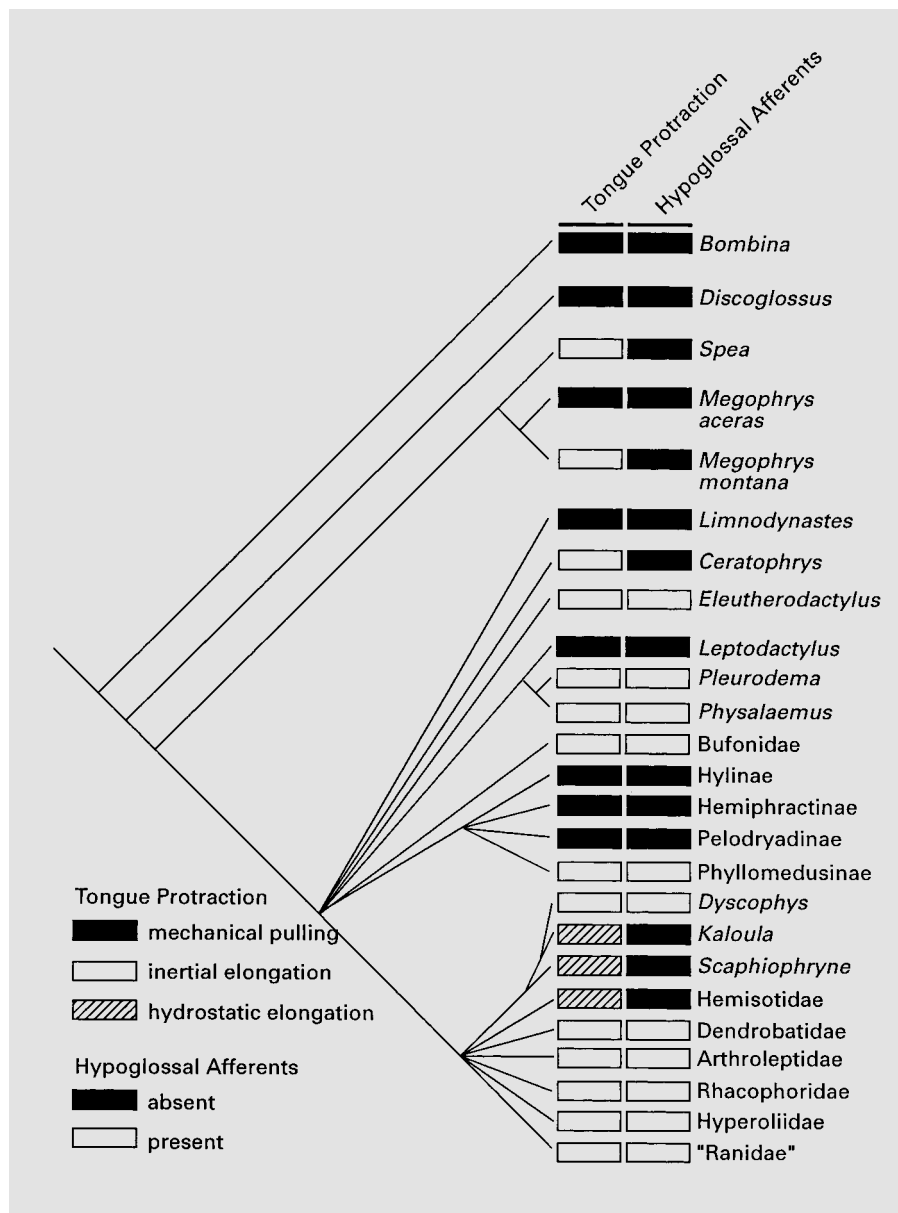
traction as the protractor muscles contract, pulling the tongue pad forward [Deban and Nishikawa, 1992]. Movements of the head, jaws and tongue are relatively small, slow and asynchronous but tongue movements can be corrected in progress within a single gape cycle. Forward dynamic models of tongue projection in frogs demonstrate that the movement is dynamically stable, and that more than 90% of the force for tongue movement comes from transfer of angular momentum from the opening jaws to the tongue [Mallett et al., 2001].

Ballistic tongue projection has evolved as many as eight times independently in anurans from ancestors that used mechanical pulling to protract the tongue (fig. 2). During ballistic tongue projection, momentum transferred to the tongue from the opening jaws produces tongue elongation of up to 210% of resting length. The tongues of inertial elongators are morphologically similar to those of mechanical pullers, except that relative tongue mass is smaller and the fibers of the tongue protractor and retractor muscles are relatively longer in inertial elongators.

Inertial elongation involves extremely rapid acceleration of the jaws and tongue at rates approaching 600 m/s². Our current research focuses on how frog jaw muscles achieve the high in vivo strain rates that are necessary to propel the tongue out of the mouth at high speeds. It appears that the depressor mandibulae muscles and/or their connective tissues store elastic strain energy prior to movement and that recovery of some of this energy amplifies the power of mouth opening [Lappin et al., 2002].

Afferent neurons with axons that travel to the brain in the peripheral hypoglossal nerve have evolved convergently as many as 4–5 times among anurans with ballistic tongue projection (fig. 2). These sensory neurons innervate epithelial mechanoreceptors of the tongue pad [Harwood and Anderson, 2000]. We hypothesize that these mechanoreceptors play a role in coordinating activity of antagonistic muscles during energy storage prior to mouth opening, and in triggering recovery of stored energy during mouth opening. In all anurans that possess them, hypoglossal afferents modulate the phase of activity of the mouth opening and closing muscles [Nishikawa and Gans, 1992; Anderson and Nishikawa, 1993; Monroy et al., 2001]. In intact frogs, the mouth opening muscles are activated before the mouth-closing muscles, whereas in deafferented frogs, mouth opening and closing muscles are activated simultaneously. Thus, when deafferented frogs attempt to feed, their mouths remain closed. By modulating coactivation of the antagonistic mouth opening and closing muscles, hypoglossal afferents likely control the storage and recovery of elastic strain energy by the mouth opening muscles, which boosts the power of mouth opening and tongue elongation [Lappin et al., 2002].

Vertebrates primitively possess purely motor hypoglossal nerves [Ariens-Kappers et al., 1936], although hypoglossal afferents have evolved independently in a number of vertebrate lineages including birds [Wild, 1990] and mammals [Lowe, 1981] as well as among frogs. It is interesting that the embryonic source of hypoglossal afferents differs among anuran lineages [Nishikawa, 1999]. In toads (family Bufonidae), hypoglossal afferents are re-routed glossopharyngeal afferents that ascend to higher brain centers in the solitary tract. In frogs (family Ranidae), they are re-routed cervical spinal afferents that ascend in the dorsomedial funiculus and project to both the granular layer of the cerebellum and the medial reticular formation [Anderson and Nishikawa, 1997].

Ballistic tongue projection has evolved numerous times independently among frogs, as have mechanosensory afferents that modulate the activity of antagonistic jaw muscles. It seems likely that afferent modulation of muscle coactivation boosts the power of mouth opening and tongue elongation by optimizing muscle coactivation for storage and release of elastic strain energy. Toads use solitary afferent pathways for this purpose, whereas frogs use spinal afferents. The function of these afferents appears to be quite similar in the different taxa, which may imply a functional constraint. Anatomically, the circuits are quite different and we are currently exploring physiological differences that might affect function. As in the case of electric fishes, relatively small changes in existing afferent pathways have led to the emergence of a novel function, modulation of the activity of antagonistic jaw muscles in inertial elongators. Likewise, convergent evolution of hypoglossal afferents among anurans with ballistic tongue projection is based on small changes in the peripheral and central connections of sensory neurons that modulate jaw muscle activity.

Sound Localization in Owls

Among vertebrates, only owls have evolved asymmetrical ears. Asymmetrical ears function to determine the vertical position of a sound source [Moiseff, 1989]. Owls with symmetrical ears are reluctant even to fly in total darkness, whereas owls with asymmetrical ears readily capture prey in total darkness [Payne, 1971]. Whereas cladograms are available for genera of weakly electric fishes [Alves-Gomes, 1999; Sullivan et al., 2000] and for families of anurans [Ford and Cannatella, 1993], less information is available concerning the phylogenetic relationships of owl genera [Randi et al., 1991; Rebholz et al., 1993]. To analyze the evolution of sound localization in owls, ear asymmetry data from Norberg [1977] were mapped onto a phylogeny (fig. 3) based on available allozyme and karyological data [Randi et al., 1991; Rebholz et al., 1993].

According to Norberg [1977], *Athene*, some *Bubo*, some *Strix*, all *Otus*, and all *Ninox* have symmetrical ears, whereas *Aegolius*, some *Bubo*, some *Strix*, all *Asio*, and all *Tyto* have asymmetrical ears. If one looks only at the evolution of asymmetrical ears, the hypothesis that ear asymmetry was lost repeatedly among owls is equally parsimonious with the hypothesis that asymmetrical ears were acquired repeatedly among owls. Thus, it is not possible to say definitively whether asymmetrical ears evolved once in the common ancestor of owls and were lost several times independently, or alternatively, whether ear asym-
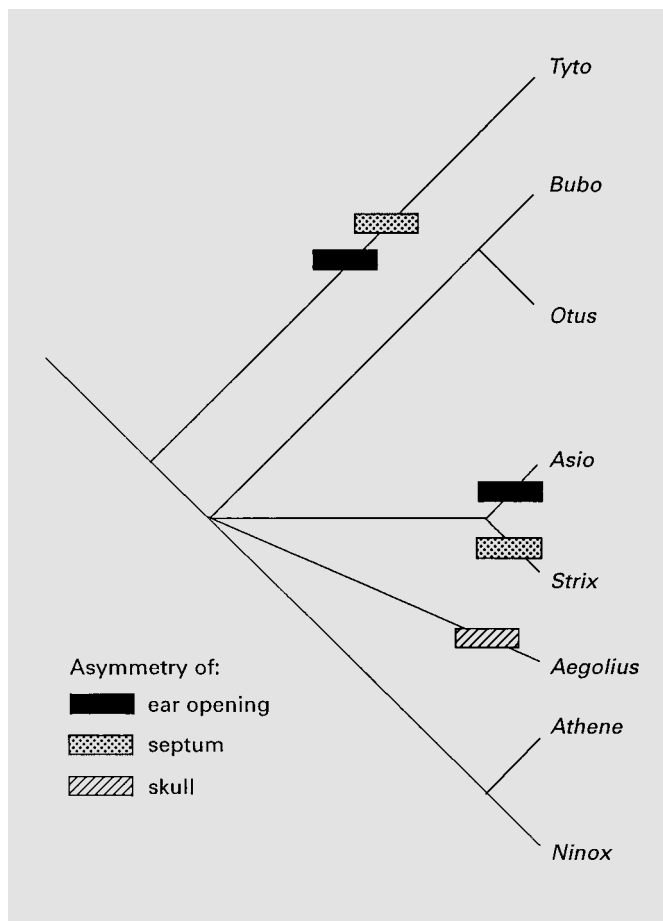
Fig. 3. Cladogram illustrating convergent evolution of ear asymmetry among owls [based on Norberg, 1977; Randi et al., 1991; Rebholz et al., 1993]. *Tyto* and *Asio* possess asymmetries of the soft tissues of the ear opening, and *Tyto* and *Strix* possess asymmetries of the septum. Only *Aegolius* possesses asymmetries of the cranium. Intrageneric variation (not shown) is present in *Bubo* and *Strix*. Given this level of variation in ear anatomy, ear asymmetry may have evolved as many as seven times independently among owls.

metry evolved convergently among owls. However, as noted by Norberg [1977], ear asymmetry differs anatomically among owl lineages (fig. 3). *Tyto*, some *Bubo*, and some *Asio* possess asymmetries in the soft tissues of the ear opening, *Tyto* and some *Strix* possess an asymmetrical septum within the ear opening, and *Aegolius* are unique in possessing an asymmetrical skull. Therefore, the most parsimonious hypothesis is that asymmetrical ears evolved at least four times and perhaps as many as seven times independently among owls. This fact is amazing, considering that no other vertebrates have evolved asymmetrical ears.

All terrestrial vertebrates use binaural cues to localize sounds in space [Fay, 1988]. Species with symmetrical ears, including humans, use both interaural time difference (ITD) and interaural intensity difference (IID) to encode the azimuth of a sound source. In contrast, owls with asymmetrical ears use ITD to encode sound azimuth and IID to encode sound elevation [Volman, 1994]. At the behavioral level, differences in ear morphology and sensory processing in owls with asymmetrical ears translate into the ability to capture prey in total darkness using acoustic cues alone, whereas owls with symmetrical ears are reluctant to fly in total darkness. Neuroanatomically, however, relatively few differences in auditory pathways are responsible for the behavioral difference.

In birds, differences in arrival times of a sound at the two ears are computed by coincidence-detecting neurons in the brainstem nucleus laminaris, which receive delay-line inputs from phase-locked cochlear neurons [Carr and Konishi, 1990]. The dendrites and synaptic channels of laminaris neurons are highly specialized for detecting submicrosecond time differences [Carr et al., 2001]. Laminaris neurons also translate the time code (phase-locked spikes from the cochlear nucleus magnocellularis) into a place code, in which ITD is represented as the position of neurons within the nucleus magnocellularis [Carr and Friedman, 1999]. This same basic organization of the nucleus laminaris is found in chickens as well as owls, and presumably represents the plesiomorphic condition. The major difference in the organization of the nucleus laminaris between chickens and owls is that in the chicken, the place-map is a monolayer of approximately 1,000 laminaris neurons with a single representation of ITD, whereas barn owls *(Tyto)* possess approximately 10,000 laminaris neurons and multiple representations of ITD [Carr and Friedman, 1999].

Likewise, there are relatively few differences in the organization of the inferior colliculus in owls with symmetrical vs. asymmetrical ears [Volman and Konishi, 1990]. In the midbrain inferior colliculus, maps of auditory and visual space are in register. In both great horned owls (symmetrical ears) and barn owls (asymmetrical ears), the auditory and visual maps of azimuth are oriented anteroposteriorly in the inferior colliculus. In both species, inferior colliculus neurons are tuned to interaural time (ITD) and intensity differences (IID) independent of frequency. In fact, the broad frequency tuning of inferior colliculus neurons appears to represent convergence of frequency-tuned neurons, which may eliminate ambiguities in the interpretation of ITD and IID. In both species, neurons in the inferior colliculus are tuned to

either ITD or IID, but not both. The chief differences between great horned owls and barn owls are in the elevation selectivity and narrower tuning of inferior colliculus neurons to interaural intensity differences [Volman and Konishi, 1990].

In summary, asymmetrical ears have evolved numerous times independently among owls. Similar auditory pathways are present not only among owls but also among birds generally. However, the auditory pathways are used for different purposes in different species. For example, all owls possess neurons that are selective for interaural intensity differences (IID) and all owls use this information for sound localization. However, owls with symmetrical ears use IID as an additional azimuth cue, whereas owls with asymmetrical ears use it as an elevation cue. In general, brain nuclei involved in the processing of binaural auditory cues are also similar between owls with symmetrical and asymmetrical ears, except that owls with asymmetrical ears have both greater acuity of sound localization and more neurons devoted to auditory processing. In this system, as in the others, small changes in existing neural pathways appear to underlie the emergence of novel abilities, such as the ability to catch prey in total darkness using auditory cues alone.

Conclusions

Collection of neuroanatomical, neurophysiological, and neuroethological data can be extremely time-consuming even for a single species. Thus, it is not surprising that neuroethology has relatively few comparative case studies in which the anatomical and physiological bases for interesting behavior patterns can be studied within an evolutionary framework [Nishikawa, 1997; Phelps, 2002]. Three relatively well studied examples are electric communication among gymnotiform and mormyriform fishes, prey capture in frogs and ear asymmetry among owls. Given the relative paucity of case studies, it is remarkable that these three examples reveal such similar (not to say convergent) patterns of brain evolution.

First, it is clear that novel behaviors have evolved many times independently in taxa whose common ancestors lack the behavior, from jamming avoidance, to ballistic tongue projection, to nocturnal prey capture. The list of behaviors and brain structures that have evolved convergently is growing rapidly (see Introduction). It is now clear that convergence is as pervasive in nervous systems as it is in the rest of the biological world [Wray, 2002], notwithstanding some claims to the contrary that nervous systems might evolve more conservatively than other biological substrates.

Second, it is apparent that novel behaviors, absent in ancestors, can be conferred by surprisingly small changes in existing neural pathways [Nishikawa, 1997; Katz and Harris-Warrick, 1999]. Why can *Eigenmannia* increase or decrease its EOD to avoid jamming, whereas *Apteronotus* can only decrease it? Why can frogs with inertial elongation open their mouths 18 times faster than mechanical pullers? Why can barn owls capture prey in total darkness whereas great horned owls cannot? Why do humans possess vocabularies on the order of 100,000 words, whereas the most highly trained chimpanzees have difficulty acquiring a vocabulary in excess of 500 'words' [Kandel et al., 2000]? It was long believed that Wernicke's (speech) area in the neocortex was the only new structure to appear in the brain during human evolution [Geschwind, 1965]. However, it now appears that even this structure has a homologue in macaques and other primates [Deacon, 1988]. Small changes in neural pathways can lead to dramatic changes in an organism's abilities, and it is clear that brain evolution at this small scale is quite common.

The behavioral importance of small scale changes on one hand, and the pervasiveness of convergent evolution on the other, have several implications for understanding brain evolution. First, similar abilities may be conferred by convergent rather than homologous circuits, even among closely related species. One example is the proprioceptive afferents that trigger ballistic tongue projection in frogs *(Rana)* and toads *(Bufo)*. Furthermore, closely related species may use the same information in different ways (as in the case of IID-tuned neurons in the inferior colliculus of barn vs. great horned owls), or they may use different ways to obtain the same information. It is difficult to avoid the conclusion that brains are probably more finely tuned to the ecology and natural history of a species than we think.

One reason that convergence is so common in the biological world may be that the evolutionary appearance of novel functions is associated with constraints, for example in the algorithms used for a given neural computation. The time-coding circuits of weakly electric fishes, birds, and mammals are a case in point [Carr and Friedman, 1999]. In all of these sensory systems, timing information is coded by phase-locked spikes and is processed in parallel with other stimulus features. These time-coding circuits exhibit a number of specializations that permit the neurons to resolve sub-microsecond time differences [Kawasaki, 1997; Carr and Friedman, 1999; Carr et al., 2001, Carr and Soares, 2002].

From these case studies, it is clear that comparative phylogenetic analyses have a lot to tell us about the nature of brains and the rules for their transformation.

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