Convergence: Obstacle or Opportunity?

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Evolutionary convergence is a remarkable phenomenon that spans all levels of biological organization. Examples are ubiquitous, and often involve correlated changes in molecules, morphology, physiology, and behavior. Birds and mammals convergently evolved the ability to regulate their body temperature, an adaptation that involves a suite of changes in physiology and anatomy, and has enabled both groups to expand into niches not available to many exothermic animals. Bats, birds, and some insects have acquired flapping flight independently, and again some of the underlying changes and resulting abilities are remarkably similar. Some bats, dolphins, and teleost fishes send out signals that produce echoes used to localize objects in the environment. What can we learn about neurobiology and behavior by investigating such phenomena?

Light-detecting eyes have evolved repeatedly in different animal phyla. Many elements of eye structure are convergent; for example, lenses have evolved repeatedly, presumably because the ability to form an image can be adaptive for many organisms inhabiting a variety of niches. Similarly, the ability to discriminate different wavelengths of light reflected by objects in the environment (color vision) has evolved repeatedly, perhaps as an adaptive trait that allows for improved selection of food items or more elaborate intraspecific communication [Pichaud et al., 1999]. The repeated origin of these features provides opportunities for us to test hypotheses concerning the pressures that have given rise to these features, and the function of each. Are these examples of convergence due to functional demands, mechanical constraints related to the physics of light, or the repeated deployment of a network of developmental genes? Are these three explanations of convergence mutually exclusive? The papers contained in this volume explore these questions through detailed analysis of a wide range of examples.

In organizing this workshop and compiling this volume, our goal is to urge comparative neurobiologists to consider the heuristic value of evolutionary convergence (homoplasy) in helping us understand the diversity of structure and function in the nervous system; that is, we want to encourage our colleagues to view convergence as an *opportunity* rather than an *obstacle* [Brooks, 1996]. We contend that a close examination of instances of evolutionary convergence can provide a wealth of information concerning processing strategies used by the nervous system, as well as constraints on neural architecture.

Convergence is a complex and important topic that spans taxa, levels of analysis, and approaches to studying the nervous system. It has been the subject of much recent interest in evolutionary biology, including a volume of papers that address the challenges and opportunities afforded by convergence [Sanderson and Hufford, 1996]. In 'The Crucible of Creation', Simon Conway Morris strives to refute the popular belief that evolutionary processes

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produce essentially random patterns, and presses the argument that the appearance of animals with human-like intelligence was inevitable; that, had we not appeared, some other organism would have evolved many of the same behaviors that we display [Conway Morris, 1998]. Although many of the best-known examples of convergence are morphological, convergence occurs at every level of biological organization. In this volume, the authors consider examples of convergence at the level of molecules, physiology, anatomy, and behavior.

The volume begins with an overview of convergence in the nervous system and behavior, provided by a consideration of three striking examples of convergent evolution among closely-related species. Nishikawa [2002] describes evidence that asymmetrical ears have evolved repeatedly among owls, a specialization that is unique among vertebrates. This asymmetry affords greatly improved sound localization, allowing owls to hunt in near-dark conditions. She considers another example well-known to comparative neurobiologists: the repeated origin of electroreception in teleost fishes, and the convergent circuitry and behavior that allow electrolocating fishes to avoid jamming signals from nearby conspecifics. Finally, she describes the repeated evolution of tongue projection in anuran amphibians. Different taxa use different morphological and neural specializations to thrust the tongue forward, but all of these specializations allow frogs to catch prey at a distance. This paper points out the widespread nature of convergence, even among closely-related animals, and raises interesting questions about the mechanisms underlying repeated evolution of similarity within narrow taxonomic groups.

Next, Zakon [2002] tackles the problem of convergence at the molecular level. Following a scheme proposed by Doolittle [1994], he points out that molecules can converge in different ways: they can develop similar functions, mechanisms of action, structures, and/or sequences. Using examples drawn from neurobiology, such as the opsin genes underlying color vision in primates, Zakon considers the roles that different types of convergence may have played in the evolution of molecules. Some of the examples lead to surprising conclusions. When a neurotransmitter has both ionotropic and metabotropic receptors, is the existence of these receptors an example of convergence? New evidence suggests that the ionotropic and metabotropic glutamate receptors share a homologous glutamate-binding region, and that a recombination event involving G protein-coupled receptors led to the subsequent divergence in the structure and function of these two receptor types. Animals like scorpions and

cone snails produce large numbers of neurotoxins, leading Zakon to suggest that a convergent *strategy* of high rates of gene duplication and recombination might govern the evolution of large gene families.

The organization and evolution of mammalian cortex is a subject of perennial interest in comparative neurobiology, despite (or perhaps because of) severe limitations imposed by availability of material. Kaas [2002] describes the organization of visual cortex in primates and their near relatives, tree shrews. Tree shrews are often used as an outgroup for comparison with primates, and features found in tree shrews are frequently assumed to represent the plesiomorphic condition. By comparing tree shrews to grey squirrels, which are not closely related but inhabit a remarkably similar niche, Kaas demonstrates that tree shrews possess many specializations that are probably specific adaptations related to their diurnal, arboreal lifestyle. The insights gained from this comparison illustrate that convergence can be useful even to researchers whose goal is to investigate homologous features, in both obvious and not so obvious ways. Certainly, by examining taxa inhabiting similar niches, researchers can distinguish convergent features, and remove these from consideration as homologues. However, if convergence is as widespread in the nervous system as suggested here, researchers investigating animals that are difficult to study may choose to examine convergent features in ecologically similar taxa for some purposes.

Continuing the theme of convergence in sensory systems, the following two papers analyze examples of convergence in the olfactory and auditory systems. First, Eisthen [2002] analyzes features of olfactory systems in different phyla that appear to present clear examples of convergent evolution, and which have been the subject of much discussion among olfactory neurobiologists: odorant binding proteins, odorant receptor molecules, signal transduction strategies, and glomerular neuropils in the central nervous system. By considering the detailed structure and function of these features, she illustrates that convergent features may arise through a combination of adaptation and constraint, and that few features constitute 'pure' adaptations. The lesson here is that neurobiologists should not assume that convergent features represent adaptive mechanisms that have arisen in response to a particular problem, and should keep in mind the other forces that may be at work.

The organization and function of the auditory system is considered by Carr and Soares [2002]. They propose that the circuitry that underlies sound localization in birds and mammals represents convergent evolution

Fig. 1. When hunting, owls use extremely small differences in the time and intensity of sounds arriving at each ear to localize a sound source, such as a mouse. Mice and other mammals use similar circuitry and computations to localize sounds, such as those produced by the flapping wings of an approaching owl. New data suggest that the mechanisms underlying time coding have evolved convergently in birds and mammals [see Carr and Soares, 2002]. AVCN = Anterior ventral cochlear nucleus; ITD = interaural time difference; MSO = medial superior olive; NL = nucleus laminaris; NM = nucleus magnocellularis.
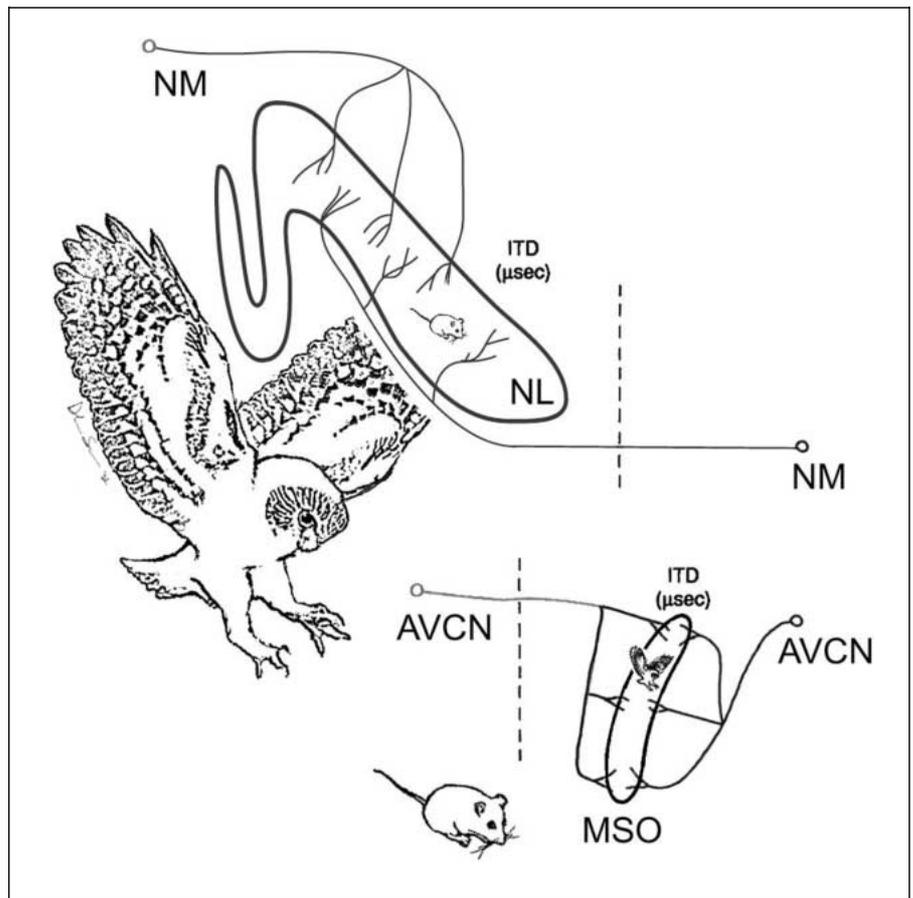
(fig. 1), rather than reflecting underlying homology, as is commonly assumed. Their hypothesis rests on two lines of evidence: the probability that tympanic ears evolved independently in the ancestors of birds and mammals, as described by Clack in a previous Karger Workshop [Clack, 1997]; and new data demonstrating that the cellular interactions involved in precise time coding, which underlies sound localization, are different in birds and mammals. It is astonishing that fine specializations, such as the shedding of dendrites in favor of a calyx-like terminal that envelops the soma of the postsynaptic cell, can evolve repeatedly to perform the same function in different animals, and should cause us to question many of our assumptions about homology of circuitry in different taxa.

Bell [2002] takes the analysis a step further in his consideration of cerebellum-like structures in the hind- and midbrain of all classes of vertebrates. The cerebellum, octavolateral nuclei in some aquatic vertebrates, electrosensory lobes in some electric fish, dorsal cochlear nucleus in therian mammals, and other structures display a similar organization in which sensory information is mapped topographically in a deep layer and Purkinje-like cells that make synapses in this deep layer interact with a more superficial array of fibers that are oriented in parallel. The general function of these structures seems to be to monitor sensory input related to motor activity, and to subtract predictable signals produced by the animal's own motor output. Such structures are present in all vertebrates, and some groups have many such structures, prompting Bell to exclaim in his talk that 'mormyrids are a cerebellum festival.' Interestingly, all these structures arise developmentally from the alar plate and are found in mid- and hindbrain, leading Bell to suggest that similar developmental mechanisms, including similar genetic networks, must underlie the development of cerebellum-like structures. If so, does this mean that these structures are, on some level, homologous?

The answer to this question is provided by Wray [2002]. In his paper, Wray takes a 'ground-up' approach

in which he considers examples provided by developmental regulatory genes that are expressed in a similar fashion in diverse animals, and then asks whether the resulting structures are homologous. For example, the gene distal-less is expressed repeatedly in tips of appendages and other structures that protrude from the body; it is clear that the tube feet of echinoderms, the limbs of vertebrates and arthropods, and the siphons of ascidians are not homologous, despite their use of distal-less during development. A simple explanation is that such developmental mechanisms might function like modules that can be deployed at different times in different places to produce particular types of structures, and that we cannot infer homology based simply on similar patterns of gene expression. This conclusion has important implications for comparative neurobiologists, and should be considered when assessing ideas such as the popular claim that eyes in insects and vertebrates are homologous because the *Pax-6* gene plays an important role in their development [Harris, 1997]. In addition, Wray considers the evolution of life-history strategies in sea urchins, and demonstrates that the adoption of a non-feeding larval stage has led repeatedly to similar larval morphology, at least among closely-related animals. Overall, the examples presented in this paper demonstrate that convergence can affect development at all levels of organization, and that similarities in aspects of development should not be given special weight when trying to assess homology.

A few overarching themes emerge from the papers presented in this volume. The most obvious is that convergent features arise in response to similar processing demands, and that many features of the nervous system that are assumed to be homologous at first glance may prove to be convergent on closer examination. Convergent mechanisms may be easier to recognize when the functional demands are well understood: many of the papers in this volume discuss examples of convergence in sensory systems, where the input and function are clear. Similar structures can evolve independently even among very closely-related animals, perhaps in part due to the availability of similar substrates on which similar developmental mechanisms can operate. Finally, convergence operates at all levels of biological organization, and features that are convergent at one level might reflect pressures operating at another level.

Convergence is not simply the inverse of homology, an annoyance that creates confusion when trying to discern patterns of homology in comparative studies. Convergence can also provide enlightenment by drawing our attention to features of the nervous system that are associated repeatedly with specialized functions, suggesting mechanisms by which the nervous system processes information and produces behavior.

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