Further Section

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Brain Behav Evol 1997;50:5-7

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Preface

Garstang [1922] recognized the importance of development in producing phylogenetic patterns of morphological change. His insight was that the evolution of ontogenetic trajectories leads to the production of novel adult forms. Whereas Haeckel [1866] emphasized the adult form and believed that ontogenetic stages of derived forms resemble adults from more primitive groups, Garstang [1922] recognized that new adult forms must arise from new ontogenetic trajectories. Thus, morphological variation must be understood in terms of the evolution of new developmental programs rather than in terms of the evolution of new adult forms [Northcutt, 1990, 1992].

Recently, a shift in emphasis from adult endpoints to ontogenetic trajectories has taken place simultaneously in several different fields, which provides a new framework for synthesis:

Genetics: The last few years have witnessed a change in the concept of mutation, from a static view that mutations form the basis of differences in adult phenotypes, to an ontogenetic view in which mutations represent novel ontogenetic trajectories [Atchley et al., 1990].

Phylogenetic Analysis: In phylogenetic analysis, morphological or neurological characters are mapped onto an independently derived cladogram. From these data, ancestral states can be reconstructed and evolutionary transitions from ancestral to derived states can be identified [Northcutt, 1984, 1985, 1986]. Like the concept of mutation, the concept of characters in phylogenetic analysis is changing from characters that include only adult phenotypes, to ontogenetic characters in which the unit of analysis includes the entire ontogenetic trajectory of a characteristic [de Queiroz, 1985].

Comparative Neurology: Phylogenetic analysis has been used to identify evolutionary transitions in neural systems [Northcutt, 1984, 1985, 1986; Roth et al., 1993; Nishikawa et al., 1992]. Most studies have proceeded within the traditional, adult-biased framework, but a few recent studies have analyzed ontogenetic trajectories as well [Northcutt, 1990, 1992].

Developmental Neurobiology: Due to recent advances in molecular biology, much has been discovered about the molecular and cellular basis of neural development in recent years [Purves and Lichtman, 1985]. One major goal of these studies is to understand how genes and their products regulate morphogenetic events during development [Meyer et al., 1987, 1988; Edwards et al., 1989; Giangrande and Palka, 1990]. Mutations in genes that control these processes alter the developmental fate of neurons, and thus the adult phenotype [Lofberg et al., 1989].

A synthesis of comparative neuroanatomy, developmental neurobiology and phylogenetic analysis may provide new insights into the evolution of neural systems [Northcutt, 1990, 1992]. Within the framework of this synthesis, three major questions about the evolution of neural systems can be addressed: (1) What are the major morphological transformations that have occurred during evolutionary history? (2) What genetic and developmental changes are associated with the transitions? and (3) What are the functional or behavioral consequences of these developmental changes?

The participants in this symposium have addressed these questions in their work on diverse model systems. The first two presentations dealt with a major evolutionary transition in the realm of invertebrates - the evolution of flight among insects. John Edwards discussed the evolutionary transition from escape behavior to flight in insects; and Michael Dickinson, Susannah Hannaford and John Palka examined the mechanics of insect wings and their sensory apparatus, and the implications of these for the evolution of flight. The second group of talks was focused on the evolution of vertebrate nervous systems: Glenn Northcutt discussed the phylogenetic consequences of ontogenetic changes in lateral line placodes; Bernd Fritzsch discussed the evolution of the octavolateralis system; and with my

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coauthors Gerhard Roth and David Wake, I discussed the evolutionary reduction of the salamander brain and the phenomenon of paedomorphosis.

Although some neurobiologists seem to proceed as though the neural circuits they study have been engineered especially for a particular function, existing neural systems are in fact descended from ancestral systems that have been modified to serve new functions [Northcutt, 1984; Dumont and Robertson, 1986; Cohen, 1988]. How neural circuits are modified during evolution is a fundamental question of neurobiology [Ebbesson, 1984; Edwards, 1985; Arbas et al., 1991]. Neural systems evolve primarily through changes in the properties of neurons (e.g., neurotransmitters and receptors), changes in patterns of activity, and/or changes in connections with other neurons. Both vertebrates and invertebrates possess nervous systems that exhibit a high degree of conservatism in their morphology. For invertebrates, it has been suggested that the evolution of the nervous system has involved tinkering with the connections among a conserved set of neurons [Edwards and Palka, 1991]. Although neuronal identity is less clear cut in vertebrates, the evolution of the vertebrate nervous system also may be characterized as tinkering within a conservative bauplan.

Several themes emerged from the symposium. Not surprisingly, the evolution of both vertebrate and invertebrate nervous systems has involved the acquisition of novel characteristics by modification of an ancestral developmental program. For example, it now appears that insect wings evolved from portions of legs originally used for swimming [Dickinson et al., 1994], and that neural circuits controlling

flight may have evolved from escape circuits [Edwards, 1994]. Likewise, the evolution of vertebrate and invertebrate nervous systems also has involved reduction or loss of structures, often through paedomorphosis, as observed in the flight system of some grasshoppers [Arbas, 1983a, b] and the central nervous system of salamanders [Roth et al., 1994]. Many structures, such as the vertebrate octavo-lateralis system, can only be understood as mosaics of progressive and regressive evolutionary events [Fritzsche, 1994]. Evolutionary transitions may involve changes in the pattern, sequence or timing of morphogenetic events during ontogeny. As exemplified by the lateral line system of vertebrates, evolutionary changes are not restricted to the terminal stages of development, as required by Haeckelian recapitulation, but rather may occur throughout ontogeny, with terminal, additions or deletions accounting for only about one third of all evolutionary changes [Northcutt, 1994].

The case studies included in this volume represent attempts by the contributors to understand the evolution of neural systems by synthesizing information about phylogeny, development and function. It is clear from these contributions that this type of synthesis has provided new insights into the evolution of neural systems, and offers great potential for the future. I would like to thank the contributors for their participation in the symposium, and the Division of Vertebrate Morphology and the Neurobiology Interest Group of the American Society of Zoologists for their sponsorship.

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Nishikawa

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