NODAL EVENTS IN FOREBRAIN EVOLUTION

by

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SUMMARY

Concepts of brain evolution within a group of animals depend upon an understanding of the phylogenetic relationships of the animals themselves. Classic concepts based upon a linear or "scala naturae" model of vertebrate evolution resulted in linear models of forebrain evolution involving sequential addition of components such as "archicortex", "paleocortex" and "neocortex". This paper examines forebrain evolution in amniotes in the context of an amniote phylogeny based on modern techniques of phylogenetic systematics or cladistics. Analysis of forebrain characters common to all amniotes identifies a basic configuration of the forebrain with a pallium, striatum and septum. Analysis of variation of forebrain characters within those clades of amniotes with Recent representatives allows conclusions about the configuration of the forebrain at principal nodes in the amniote cladogram. Nodal patterns can be defined for mammals, turtles, lizards, snakes, crocodilians and birds. In contrast to the classic concept, the analysis suggests reptilian and mammalian patterns of forebrain organization were derived independently from a basal amniote pattern.

KEY WORDS: Phylogenetic systematics, cladistics.

INTRODUCTION

The forebrain consists of the diencephalon and telencephalon, two derivatives of the vertebrate neural tube believed to play major roles in complex behaviors. Because of its likely role in behavior, there has been considerable interest in tracing the evolutionary history of the vertebrate forebrain. However, there has been only a gradual realization of the extent to which evolutionary scenarios describing forebrain evolution depend upon specific assumptions about the phylogenetic relationships of the animals under consideration. This paper makes the simple point that our concepts of vertebrate phylogeny have a direct impact on our concepts of brain evolution and organization. It briefly outlines two models of vertebrate forebrain evolution that have been popular in the past, and then explores the implications for our concepts of forebrain evolution of vertebrate phylogenies derived by the methods of phylogenetic systematics or cladistics. This involves what I will call a "nodal analysis" in that the branching pattern, or cladogram, that expresses a hypothesis about vertebrate relationships
consists of a series of nodes. Given space restrictions, the analysis is brief and restricted to amniotes. Detailed treatments of specific topics are available in recent reviews (ULINSKI, 1983, 1986, 1990a, b; ULINSKI & MARGOLIASH, 1990). The discussion comments on the results of this analysis as compared to the more traditional models.

MODELS OF FOREBRAIN EVOLUTION

Figure 1 illustrates three models that relate forebrain evolution to the pattern of vertebrate evolution. Figure 1A summarizes a model of forebrain evolution introduced by ARIENS KAPPERS (1921). Like most workers of the time, Ariens Kappers accepted a "scalae naturae" or "phylogenetic scale" concept of vertebrate evolution (see Hodos & Campbel, 1969) in which vertebrate groups are arranged along a linear scale with "lower" vertebrates being simpler and "higher" vertebrates more complex. It is not surprising, then, that Ariens Kappers proposed a linear model of forebrain evolution in which some components (a in fig. 1A) are present in "lower" vertebrates and evolution proceeds by the addition of components (b and c) at successive stages of evolution. For example, an important implication of the model is that, since mammals evolved from reptiles, the forebrain of mammals is viewed as having evolved from a reptilian configuration by the addition of components not present in reptiles (such as neocortex). A ambiguity in the model is how the brains of extinct or ancestral forms should be incorporated into the scheme. It is clear that modern mammals did not evolve from modern reptiles such as turtles, but the model does not propose an explicit algorithm for determining what the brains of the species ancestral to mammals looked like.

Fig. 1B illustrates a model derived from workers such as C. J. HER3 RICK (1948) and several later Soviet (Filimonoff, 1964; Belekhova, 1969) and Western (Diamond & Hall, 1969; Ebesson, 1980; Valverde & Facal-Valverde, 1986; Morgane et al., 1986) workers. It addresses the issue of how to relate the brains of living species to those of extinct forms by attempting to identify "key" species that have changed little since leaving the mainstream of vertebrate evolution. Considerable attention has been devoted to studies of the cerebral cortex of turtles (e.g. Ebner, 1976) because turtles were held to be closer to the origin of mammals than other reptiles and to have changed little since appearing in the fossil record, and similar arguments have led to investigations of the cortices of opossums (Ebner, 1976), hedgehogs (Kaas et al., 1970; Valverde & Facal-Valverde, 1986) and dolphins (Morgan et al., 1986; Glezer et al., 1988). Mammals are viewed as having evolved from reptiles, and