Snakes and Ladders: A Reappraisal of the Triune Brain Hypothesis

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MacLean's triune brain model of brain evolution continues to be controversial. This paper argues that while MacLean made a real contribution in his effort to link brain anatomy, behavior, and evolution, his model assumes a progressive ladder like process that is inconsistent with modern understandings of the evolutionary change. Rather we should see brain evolution as process of niche adaptation built on mosaic of conserved and derived neurological structures. MacLean's great contribution was his recognition of the existence of clade level neuroanatomic – behavioral complexes. But these structures always need to be seen in the context of a species specific environment of evolutionary adaptation.

Snakes and Ladders: A Critique of the Triune Brain Hypothesis

In its 1978 yearbook the National Society for the Study of Education published "A mind of three minds: Educating the triune brain" by neuroscientist Paul D. MacLean. In this paper MacLean explained to educators the central ideas of his triune brain hypothesis. He described the human brain as having an expanded forebrain while "retaining the basic features of three formations that reflect our ancestral relationship to reptiles, early mammals, and recent mammals" (p. 308). He labeled these three structures as the reptilian brain (R-complex), the paleomammalian brain (limbic system), and the neomammalian brain. According to MacLean "the three formations constitute a hierarchy of three brains in one, or what may be called for short a triune brain" (p. 309).

MacLean was a pioneer in efforts to integrate information from evolutionary theory, comparative neuroanatomy, animal behavior, and psychology. His model has had wide appeal and has been endorsed by educators (e.g., Nummela & Rosengrn, 1986), psychiatrists (e.g., Stevens & Price, 1996), literary figures (e.g., Koestler, 1967), and, perhaps most famously, astronomer Carl Sagan (1977).

It is important to acknowledge MacLean's contribution. He insisted that human behavior must be viewed in terms of its neurobiological roots and evolutionary origins. He understood the importance of comparative psychology and was willing to draw data from disciplines as distinct as dual process psychology and paleontology. In addition, at least one of his central contentions, the idea that some brain structures and associated behaviors are conserved across phylogenetic change is essentially correct.

Having said this, however, it is clear that the triune brain hypothesis, as stated by MacLean, is deeply flawed. The critical weakness of MacLean's model is his description of brain evolution as a ladder like process of progressive change (MacLean, 1973) and his invocation of “directional evolution” (MacLean, 1990, p. 95) ; views that are inconsistent with modern understandings of the evolutionary process (Butler & Hodos, 1996).

While evolutionary processes may appear to us as progressive, this idea is mistaken. Evolution does not, indeed can not, reach for some predetermined telos. Rather natural selection takes place in response to proximal environmental challenges. There is no scale of nature with humans on top, rather we, and all other extant organisms, exist because our ancestors enjoyed some measure of reproductive success. Fitness, in the Darwinian sense, means differential reproductive success and not any human conceived notion of progress (Williams, 1996). Indeed, it is well understood that an adaptation that raises fitness in one environment, may lower fitness after that environment changes.

It is also is well understood that selection can only operate on the materials at hand. Conserved developmental processes constrain evolutionary change. For example, almost all mammals, including giraffes, have seven cervical vertebrae (Hyman, 1974). Mammals share this feature because of they share a common ancestor. The phenomenon of similarities between organisms that result from common ancestry is called evolutionary homology (Minkoff, 1983). Evolutionary homology remains one of the main lines of evidence for evolution and is the basis for comparative anatomy.

The triune brain hypothesis claims the existence of three distinct brains achieved at three distinct stages of evolution (a reptile stage, a paleomammalian stage, and a neomammalian stage). Fish are described as relying on a “neural chassis” (p. 19) limiting them to predominately autonomic responses. Immediately we can see that the hypothesis runs into difficulty. As MaClean (1990) freely acknowledges, fish do possess a forebrain, but he argues that it is smaller relative to other brain structures when compared with the brains of “more advanced forms” (p. 21). The fact of the matter is that all vertebrates undergo a tripartite division of the nervous system early in embryonic development. Three swellings occur in the developing vertebrate brain; the prosencephalon, the mesencephalon, and the rhombencephalon (Romer, 1970). Thus, in a sense, a triune division of the brain is not a set of stages but a common vertebrate trait. According to Striedter (1998) most neurobiologists have abandoned "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" (p. 106). Natural selection acts on the variation at hand, thus these structures are modified to meet different adaptive challenges. Tempting and convenient as it is to label some animals "primitive" and others "advanced" it is always worth remembering that all extant organisms are evolutionary successes. All of their ancestors met the environmental challenges posed by the environment and passed genes on to the next generation. Fish are not less evolved than other vertebrates. Indeed, if success is measured by number of species, expansion into diverse environments, and population size, it can be argued that fish are the most successful of all vertebrates. Fish brains too have adapted and evolved and, consequently, fish exhibit many complex behaviors, including cooperation and social learning (Bshary, Wickler. & Fricke, 2002). It is now clear that MacLean's greatly underestimated the behavioral and cognitive capacities of many animals.

Critics of MacLean (Pinker, 2002, Reiner, 1990) rightly note his oversimplifications and misunderstanding of the evolutionary process but they err in dismissing in central insight; the existence of evolutionary homologies in brain and behavior. This is the valuable core of MacLean's argument that is worth preserving. It is possible to describe certain clade level neuroanatomical – behavioral complexes. A number of experts have recognized that these complexes exist (e.g., Konner, 1991; McKinney, 2000). For example, Allman (2000) tells us that "the network of serotonergic neurons in the brain stem, was present in the earliest vertebrates and has remained a remarkably anatomical constant position throughout vertebrate evolution" (p.

19). Some of the criticism of MacLean may stem from his insistence on labeling this structure a reptilian brain. Cory (2002) has proposed a needed correction: “the reptilian complex could be thought of, and perhaps redesignated, as the ancient amniote complex or even the early vertebrate complex” (p. 12).

Mammalian brains share some features with all other vertebrates (the vertebrate complex) because of common ancestry with those other organisms. Rather than a ladder of progress, phylogeny is better seen a branching structure. While fish, for example, also share the common vertebrate complex, they have continued to evolve many complex behaviors in response to particular adaptive challenges (Bshary, Wickler, & Fricke, 2002). Similarly we must reject MacLean's simple notion of a paleomammailain brain and a neomammalian brain. A more useful mode would recognize both a common mammalian complex that includes changes in the hypothalamus for thermothermoregulation (Gisolfi & Mora, 2000), the advent of the six layered isocortex (Inoue, Nakamura, & Osumi, 2001), and associated mammalian behaviors. Beyond this, different orders of mammals have differently evolved behavioral neuroanatomic complexes. Thus, it should be possible to speak of a cetacean (whales and dolphins) complex and a primate complex. Because we are primates we share in a common primate complex. Any understanding of our cognitive and behavior complexes must take this primate heritage into account. For example, many of the regularities in cognitive development first observed by Piaget are now known to be common across many primate species (Parker & McKinney, 1999). In addition, we need to understand how that primate heritage has been modified to meet the adaptive challenges of particular environmental niches. Any species, including humans, has passed through its own environment of evolutionary adaptation (Bowlby, 1982).

The important question is not: where does the human brain fall on the scale of evolutionary progress? Rather we must ask: what selective forces have shaped the human brain?

A promising answer to this question is Dunbar's (1998, 1999) social brain hypothesis. Dunbar (1998) asserts that "primates' large brains reflect the computational demands of complex social systems" (p. 178). In an allometric study of primate brain size Dunbar (1998) has found that the log of neocortex ratio (ratio of neocortex volume to remaining brain volume) explained almost 40% of the variance in log of primate group size. According to Dunbar (2003), "the cognitive demands of living in complexly bonded social groups selected for increases in executive brain (principally neocortex)" (p. 163).

The social brain hypothesis is interesting because it suggests that our environment of evolutionary adaptation was primarily social and that brains evolved to solve the problems of group living. For example, seriation, the ability to rank order objects shared by humans and other primates (Parker & McKinney, 1999) may have its roots in the adaptive challenges posed by negotiating primate dominance hierarchies (Cummins, 1998; Edelman, & Omark, 1973; Genovese, 2003).

MacLean attempted to unify neuroscience, psychology, and evolutionary theory. Although his model was flawed such an integration is still desirable. Theoretical and empirical advances in evolutionary psychology hold out the possibility that it may be obtainable.

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