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The Evolution of Reentrance in the Vertebrate Brain

Summary.

This page is a review of the evolutionary development of reentrant systems in the vertebrate central nervous system. The telencephalon of the amphibian brain exhibits a relatively undifferentiated structure, in which the cell bodies of most neurons are located near the ventricles, while the tissue near the pial (superficial) surface is composed largely of fibers. Reentrant circuitry is clearly evident in the amphibian brain, but it is based on projections between nuclei. The six-layered neocortex, which evidently evolved as a result of the integration of the reptilian general pallium and the dorsal ventricular ridge, must be viewed as a major structural innovation of the mammalian brain. This neocortical architecture may have evolved to facilitate a very powerful, nested bi-level mode of recurrent and reentrant computation. The further development of many differentiated cytoarchitectonic areas within mammalian neocortex is evidently the result of a general growth in brain size, followed by parcellation of connections according to conservative genetic rules which have been determined as the outcome of morphoregulatory processes; however, the process may hve been driven by Darwinian pressures to develop increased behavioral sophistication.

Amphibian brains.

The brain of the tiger salamander (Amblystoma) represents a living example of the amphibian brain plan. Modern amphibians appear little changed from ancient fossil amphibian specimens. Thus, the general organizational features of the brain of Amblystoma may have arisen as long as 500 million years ago, at the beginning of the Devonian age. The anatomy of this brain is described extensively in Herrick (1948). Like the mammalian brain, the brain of Amblystoma consists of a hindbrain (rhombencephalon), including the medulla oblongata and the cerebellum, with connections to the spinal cord and major cranial nerves; a midbrain (mesencephalon) including the tectum and tegmentum; and a forebrain (prosencephalon) consisting of the diencephalon (thalamus and hypothalamus) and telencephalon (cerebral hemispheres.) In the spinal cord, hindbrain, and midbrain, a division between dorsal sensory fiber tracts and ventral motor tracts is marked by the sulcus limitans. However, the anterior extent of the sulcus limitans is poorly defined, and appears to move ventrally at its rostral end; thus, the entire prosencephalon is arguably derived from the dorsal (sensory) alar plate.

Within the salamander telencephalon, areas homologous to the major divisions of the mammalian telencephalon have been identified based on their morphological relations and connectivity of major fiber tracts. These areas include the hippocampus, identified by its position in the dorsal medial wall of the hemispheres; the amygdala, just ventral to the hippocampus; the corpus striatum, on the ventrolateral wall of the hemisphere; and the pyriform cortex and primordial pallium, on the dorsal surface.

However, many of the specific adaptations of telencephalic areas which are evident in mammals are not exhibited in the amphibian brain. In general, the cell bodies of most neurons are located near the ventricles, while the tissue near the pial (superficial) surface is composed largely of fibers, both dendrites and axons. Both local and long-range axonal projections are intermingled in a dense neuropil. Within this synaptic field, Herrick notes, there is relatively little separation maintained between inputs from various sensory modalities, as the projections from the various nerve fibers are intermingled into a few common areas even at the first synapse. This is not to say that the structure of the amphibian brain is completly homogeneous; on the contrary, many of the major structures and fiber tracts of mammalian brains may be found (at least in primordial form) in Amblystoma. However, the overall structure is unmistakably much less differentiated than mammalian forms. Furthermore, even the brain stem is much less differentiated than the mammalian brain stem: even the basic structure of nuclei associated with major nerve fiber inputs, and fiber tracts interconnecting those nuclei with higher brain centers, is only primordially differentiated in Amblystoma.

Reentrant circuitry is clearly evident in the brain of the tiger salamander. In fact, two-way reentrant connections are common, and circular pathways may also be found. Herrick argues that these circuits serve to link the animal's internal motivations with its sensory and motor apparatus, and compares their function to the then-recently developed control of antiaircraft weapons by radar.

The adaptations of the neocortex which are not present in the salamander are the multi-layer differentiation of the cortex and the stylized terminations of forward connections in the granular layer. These adaptations would appear to be helpful to support the style of computation postulated by the Bayesian reentrant model.

Reptilian brains.

The origin of the order of reptiles is believed to date back to the Permian era, more than 200 million years ago. Modern representatives of this order include lizards, turtles, snakes, and crocodiles. The brain of the turtle is typical and relatively unspecialized (Johnston, 1915). Compared to the amphibian brain, the most immediately apparent differences are the greatly expanded cerebral hemispheres, and the appearance of a thickened volume of neuropil on the ventricular surface of the lateral wall of each hemisphere, known as the dorsal ventricular ridge. In some parts of the telencephalon, including the hippocampus and general pallium, the amphibian vertical structure (with cell bodies located nearest the ventricle, surrounded by fiber tracts) is still evident. The striatum and septum exhibit a more uniform distribution of cell bodies and fibers throughout the neuropil, while the pyriform cortex alone displays the three-layered structure also typical of mammalian pyriform cortex. However, in reptiles (unlike in mammals) the pyriform cortex is underlain by the dorsal ventricular ridge. The dorsal ventricular ridge exhibits a pattern of interconnections with sensory and thalamic centers which is broadly similar to some connections in mammalian sensory neocortex (Karten and Shimuzu, 1989).

The evolution of mammals.

The mammals first appeared in the fossil record approximately 190 million years ago, but did not radiate to fill a diverse variety of ecological niches until after the end of the Cretaceous period and the extinction of the dinosaurs. The lineage leading to mammals, including the therapsid and cynodont mammal-like reptiles, split off from the lineages leading to modern reptiles during the Carboniferous era, almost 300 million years ago. (Lambert et al., 1985). There are no living species which closely resemble these early mammal-like reptiles; thus, the evolutionary steps which presumably led from the reptilian brain to the mammalian brain are very difficult to trace.

Since the Paleocene radiation, a great diversity of mammalian species have arisen, exhibiting an equally great diversity of brain structure. However, all mammalian brains exhibit a number of features which are distinctive from those of any reptilian or amphibian brain. These differences extend even to the level of the medulla oblongata, where the diverse visceral and somatosensory inputs generally terminate in distinct nuclear structures which are linked by fascicular tracts to structures in the diencephalon and telencephalon. At the midbrain, the tectum is elaborated into the superior and inferior colliculi, and the hypothalamus is greatly elaborated. The differences are most evident in the cerebral hemispheres, where the relatively undifferentiated neuropil of the amphibians and reptiles is superseded by the highly specialized structures of mammalian neocortex and allocortex (limbic cortex.) The homologue of the reptilian dorsal ventricular ridge is not immediately evident in mammals; some authors have maintained that it is homologous to the mammalian amygdala (Carey, 1982; Johnston, 1915), while others argue that the cells of the dorsal ventricular ridge have migrated to become the source of the cells of the mammalian cortical plate (Deacon, 1990; Karten and Shimuzu, 1989; Mumford, 1994) and that the migration of the cells of the ependymal layer (at the ventricular surface) to the cortical plate during mammalian ontogeny may be a recapitulation of this evolutionary development.

MacLean's (1970) "triune brain hypothesis" is a broad, sweeping view of the history of vertebrate brain evolution. Maclean proposes that the primitive mammalian brain arose with the development of generalized cerebral cortex over the reptilian "R complex", and that the advanced mammals are distinguished by the further accretion of six-layered neocortex. While MacLean's view is helpful in some respects, it is also subject to a number of misinterpretations or over-interpretations. For example, the amphibian brain already includes precursors of mammalian limbic structures, and the reptilian brain includes areas in the primordial pallium which are homologous to mammalian neocortex, including their pattern of sensory projections to and from thalamic nuclei. Thus, the view that the characteristically mammalian structures were simply added to the brain late in evolution must be replaced by an interpretation in which the paleomammalian and neomammalian brains developed through a process of elaboration and differentiation from structures which already existed in the most primitive amphibian brain. Rather than thinking of the primate brain as a sort of layer cake, one might think of it as a balloon which has been stretched, more in the cortical areas than in the brain stem and limbic regions.

In the evolution of the mammalian brain from the reptilian and amphibian, very significant structural changes occur in the brain stem and mesencephalic regions as well as in the limbic system; that is, the "R system" is not strictly conserved in evolution. The exact functional significance of these changes is beyond the scope of this paper, but the idea that the mammalian brain contains within itself a complete and still-functioning reptilian core, appears to be an oversimplification.

Discussions of the "limbic lobe" as a functional unit (i.e. MacLean's "paleomammalian brain") should not obsure the fact that the limbic system consists of several structures with very distinctive evolutionary origins and cellular makeup. The pyriform cortex is possibly the least derived structure (most closely resembling its primordial origins) and is still involved with its original olfactory function. The hippocampus, by contrast, is a highly derived, multilayer structure (together with the dentate gyrus) which also exhibits an innovative biochemistry for long-term potentiation in mammals. Because of its connectivity, the cyngulate gyrus is considered part of the limbic system, but by cytoarchitectonic criteria, the cyngulate gyrus is fully developed six-layered neocortex.

Both the neocortex and the limbic system must be viewed as a major structural innovations of the mammalian brain. As MacLean noted, the structures of the limbic system have been largely conserved throughout mammalian evolution. However, it is also important to note that all species of mammals have significant areas of six-layered neocortex (as well as limbic cortex). While important differences exist between the cortex in different areas of the brain, and among mammalian species, nevertheless it is believed that the similarities outweigh the differences (Braitenberg and Schuz, 1991).

Cortical evolution.

Kaas (1990) notes an evolutionary trend towards increasing numbers of specialized areas in mammalian neocortex in animals of increasing size. For example, while the hedgehog has only 8 clearly defined regions in its cortex, the cat has at least 24. Along with this increase in structural complexity is an increase in behavioral sophistication. This trend continues in primates. Felleman and Van Essen (1991) identified at least 32 distinct areas in Macaque monkey visual cortex, interconnected by as many as 300 reentrant fiber projections. Whether or not this upward trend continues in man is not completely clear at this time. Brodmann's cytoarchitectonic maps of humans and monkeys (reproduced in Pandya et al, 1988) show similar areal divisions in visual cortex, but an increased level of complexity in areas related to hearing and language in the human. Brodmann's map of monkey visual cortex is much simpler than Felleman and Van Essen's map, which is based on electrophysiological measurements and connection studies as well as cytoarchitectonics. Many of these same studies cannot be done on human subjects.

A number of theories have been proposed to account for the trend of evolution of the mammalian brain. These theories are reviewed in Deacon (1990). An early 20th century synthesis held that the primary sensory cortical areas appeared first in mammalian brain evolution, followed by association areas (including language areas) which were inserted into the spaces between primary sensory cortex and limbic cortex. The emergent association areas were viewed as the highest, most complex and most powerful products of the evolutionary process. This view was based on arguments from homology ("primitive" mammals have primary sensory areas, but little if any associative areas) and from ontogeny (association cortex was seen as maturing later because it myelinates later.)

Pandya et al. (1988) and Sanides (1969), while accepting an additive view of the evolutionary process, proposed that the early 20th century view of the sequence of development of primary, secondary and associative cortex was inverted. Their argument was based on an alternative view of the significance of evolutionary trends in myelination: since primitive mammals exhibit little myelination, they argued that greater myelination (such as exhibited in the primary sensory and motor areas of higher mammals) is a sign of later evolutionary development. Thus, according to Sanides and Pandya's model, sensory systems evolved out of a process of differentiation of neocortical areas arising from limbic cortex. Furthermore, the neocortex is seen as originating from one of two primordial moieties: either archicortex (hippocampal cortex) or paleocortex (olfactory and pyriform cortex.) According to this model, as successive new cortical areas were elaborated during the evolutionary process, they became enervated by new projections from thalamic sensory centers. Primary and secondary auditory, sensorimotor and visual cortex were built as superstructures arising out of limbic cortex; they exist as islands of neocortex arising out of the primitive limbic structures, with few if any interconnections at primary input/output levels between the modalities. In this model, polymodal cortex exists primarily in limbic paleocortex. Thus, coupling between the visual system, auditory system, somatosensory system and the motor systems must also exist primarily at the level of limbic cortex.

As an alternative to both the early 20th century synthesis and the mechanisms suggested by Pandya et al. (1988) and Sanides (1969), Deacon proposes a symmetrical differentiation process, followed by parcellation of connections. According to this "displacement hypothesis", parcellation and invasion events are caused by competitive local factors. In this scenario, many events in the development of neocortex in mammalian evolution are the result of a general growth in the size of the cortex, followed by parcellation of connections according to conservative genetic rules which are determined as the outcome of a morphoregulatory process involving cell adhesion molecules (CAMs), substrate adhesion molecules (SAMs) and cell junctional molecules (CJMs), which regulate the development of the growth cones of axonal and dendritic projections (Edelman, 1987, 1992).

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