

# The evolutionary origin of the mammalian cerebral cortex

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The origin of the mammalian neocortex is usually considered as an improvement in the structure of the brain. Alternatively, I suggest that the mammalian neocortex arose as a consequence of contingent adaptations in which there was no specific selection for more elaborate cognitive abilities. In primitive mammals, the adaptation to nocturnal life produced a reduction of the optic tectum (superior colliculus). In addition, the development of the olfactory system triggered the development of the cerebral cortex. It is proposed that, since both the optic tectum and the cerebral cortex are laminar structures, the growing cortex replaced the tectum in many integratory functions. When mammals reinvaded diurnal niches, the optic tectum did not redevelop, and the cerebral cortex remained the main integratory and perceptual system. This is a case of irreversible reduction of an organ. In reptiles and especially in birds, although there was also an increase in brain size (associated with higher cognitive capacities), the optic tectum grew in size and complexity and the forebrain grew largely as a nonlaminar structure (except the Wulst in birds). Therefore, the origin of the cerebral cortex resulted from the combination of adaptations to nocturnality and the development of olfactory-driven behavior, and its origin is not directly related to higher cognitive capacities.

## ABBREVIATIONS

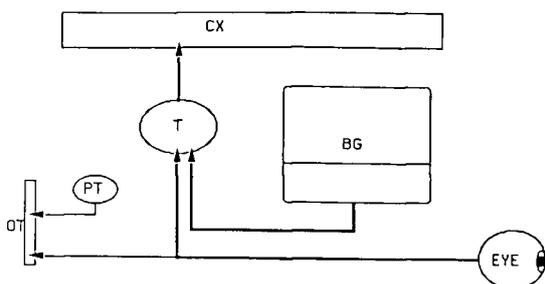
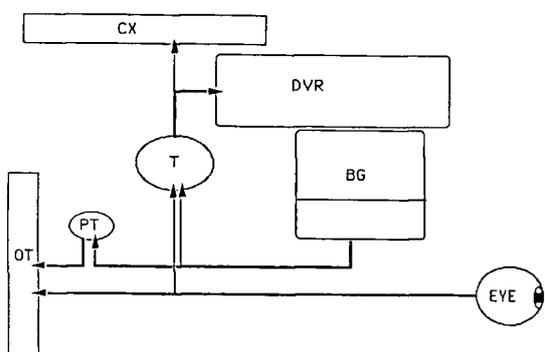
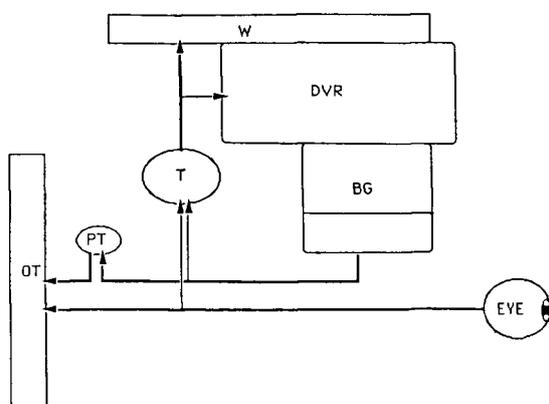
AR	Archicortex
BG	Basal ganglia
CX	Cerebral cortex
DMN	Dorsomedial nucleus of thalamus
DVR	Dorsal ventricular ridge
EN	Entorhinal cortex
FC	Frontal cortex
HP	Hippocampus
NC	Neocortex
OT	Optic tectum / superior colliculus
PC	Paleocortex
PT	Pretegmentum
PY	Pyramidal cortex
T	Thalamus
W	Wulst

## INTRODUCTION

Although all vertebrates share a common plan of brain organization, there is also diversity in more detailed aspects of brain structure (Sarnat and Netsky, 1981; Northcutt, 1981; Ulinski, 1990b). Mammals are characterized by the development of a large, laminar

neocortex that receives sensory projections from the thalamus, and a very reduced optic tectum (the superior colliculus, a laminar structure) that receives direct retinal projections (Fig. 1A). On the other hand, reptiles have developed a nuclear structure, the dorsal ventricular ridge (DVR), which is similar to the basal ganglia in terms of superficial histology and location (Fig. 1B). DVR receives most sensory thalamic projections and is considered homologous to parts of mammalian neocortex at least in terms of connectivity (Northcutt, 1981; Ulinski, 1983, 1990b). Reptiles have also retained a well developed laminar optic tectum, receiving an important proportion of the visual projections from the retina. Reptiles and amphibians have a primitive cerebral cortex, but it is not nearly as developed as it is in mammals (Ulinski, 1990a). Birds (Fig. 1C) have a slightly modified reptilian plan of brain organization (Ulinski, 1990b; Ulinski and Margoliash, 1990), with an especially large optic tectum and a reduced cerebral cortex (lateral, medial and dorsomedial). Birds have also developed a laminar structure related to the cerebral cortex (the Wulst), and their DVR is thick-

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**A****B****C**

*Fig. 1:* Highly simplified diagrams of projections from the retina and the basal ganglia in mammals (A), reptiles (B) and birds (C). Basal ganglia projections to the optic tectum via the substantia nigra are not shown. BG, basal ganglia; CX, cerebral cortex; DVR, dorsal ventricular ridge; T, thalamus; OT, optic tectum (superior colliculus in mammals); PT, pretectum; W, Wulst.

ened in relation to reptiles and retains its nuclear architecture.

For several authors, the origin of the mammalian neocortex has been implicitly or explicitly considered as a structural improvement over other types of brain organization (Papez, 1929; Jackson, 1931; MacLean, 1973; Brown, 1967, 1991; Glezer *et al.*, 1988; Allman, 1990), despite the fact that at comparable levels of encephalization, birds and mammals do not show significant differences in cognitive abilities (Hodos, 1970; Walker, 1983). Recently, Allman (1990) has proposed that the increased development of laminar structures in the brains of birds (optic tectum and Wulst) and of mammals (neocortex) are associated with exploratory behavior that develops with homeothermy. This hypothesis may explain some facts such as the larger brain size in these two groups as compared to reptiles. However, it does not account for the differences in brain structure between birds and mammals, *i.e.*, the striking reduction of the optic tectum (being a laminar structure) in mammals, and the fact that in birds DVR remains largely a nuclear structure.

In this paper, I suggest that the emergence of the mammalian cortex can be attributed more to historical circumstances than in this case resulted in an irreversible change in organization, rather than to a selective advantage in perceptual and cognitive abilities. The hypothesis proposes an explanation of the reduction of the optic tectum (superior colliculus) in mammals, and of the maintenance of a large, nuclear DVR in birds.

#### *The origin of the mammalian neocortex*

Although it may have been in an incipient state in mammal-like reptiles (Quiroga, 1980), the mammalian neocortex developed among the first true mammals (Jerison, 1973, 1990; Hopson, 1979; Quiroga, 1980; Kemp, 1982), which were small sized, nocturnal animals, superficially similar to present-day rodents and insectivores. It has been proposed that, as an adaptation to nocturnal life, mesozoic mammals did not have a strong sense of vision, resulting in a reduction of the optic tectum (superior colliculus) (Jerison, 1973).

Concomitantly, mesozoic mammals developed an elaborated olfactory system (Jerison,

1973; Kemp, 1982; Lynch, 1990). The olfactory bulbs project directly to the olfactory cortex in both reptiles and mammals (Haberly, 1990). It is likely that in protomammals, paleo and archicortical structures (receiving primary and secondary olfactory projections from the olfactory bulb; Fig. 2) became more developed in response to increasing olfactory development (Lynch, 1990; Ulinski, 1990a). It has been suggested that, in evolution, the elaboration of sensory systems may produce an expansion of the central regions receiving these projections (Woolsey and Van der Loos, 1970; Welker and Van der Loos, 1986).

The secondary olfactory afferents include, among other structures, the dorsomedial nucleus (DMN) of the thalamus, that projects to the frontal cortex, and the frontal cortex itself (Haberly and Price, 1978a, b; Haberly, 1990; Fig. 2). It is interesting that these projections seem to be better developed in primitive mammals. The DMN of the opossum (marsupial) has much denser olfactory projections than is the case in placental mammals (Benjamin *et al.*, 1982). In addition, in the echidna (monotreme), which has a highly developed olfactory system, the projection of the DMN occupies a vast area of the anterior neocortex (Welker and Lende, 1980). This evidence has in part led Lynch (1990) to propose that the increasing olfactory projections had a dominant role in the evolutionary emergence and development of the neocortex.

Mesozoic mammals also developed a sensitive audition, partly based on the acquisi-

tion of a dentate-squamosal jaw articulation, and the consequent full incorporation of the ear ossicles into the auditory system (Jerison, 1973; Kemp, 1985). In addition, there may have been increased somatosensory sensitivity associated with the loss of scales in the protomammalian lineage. Apparently, the development of these sensory modalities was associated to the growth of their telencephalic projections.

I suggest that in mammals, an additional factor favoring the growth of thalamo-cortical sensory projections (somatosensorial, auditory *and* visual) was the establishment of associative connections between these modalities and the olfactory system, which served in the cognitive elaboration of sensory stimuli. The olfactory projection forms extensive associations with the neocortex in the hippocampus and other cortical areas (Lynch, 1990). These associations may have contributed to fuse different perceptual modalities into multisensorial "objects".

These were not the only changes that occurred. In reptiles, the basal ganglia (involved in motor functions) send two major indirect projections to the optic tectum, one via the pretectum (see Fig. 1B) and the other via the substantia nigra (Reiner *et al.*, 1984; Ulinski, 1986; Medina and Smeets, 1991). Besides its optic function, the optic tectum is a principal center for the integration of complex sensory information and motor signals (Ulinski, 1983, 1986). In mammals, similarly to retinal projections, the output of the basal ganglia to the pretectum and then to the optic tectum is deviated to the thalamus (motor and intralaminar nuclei; Reiner *et al.*, 1984; Ulinski, 1986; Brauth, 1990; Fig. 1A). In reptiles there may be some projections from the basal ganglia to the thalamus (Parent, 1986), but in any case they do not seem as prominent as in mammals (Ulinski, 1990b; Brauth, 1990). Additionally, in mammals direct, descending connections from the cerebral cortex reach the reticular formation and the spinal cord, while in reptiles they never go below the basal ganglia (Ulinski, 1986). Also, in mammals there is an increase of the ascending cerebello-thalamic projections (Ulinski, 1986). Thus, the cerebral cortex of mammals engages in close relations with the basal ganglia, cerebellum, motor brainstem and spinal cord. This prob-

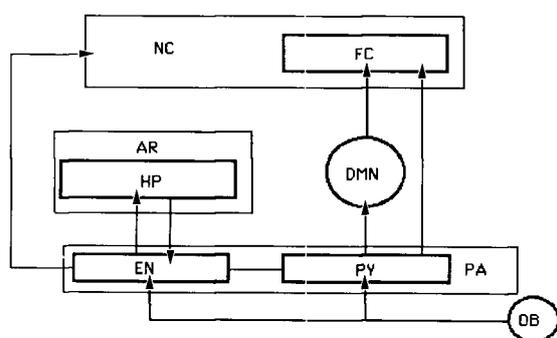


Fig. 2: Scheme of some olfactory projections in the mammalian brain. AR, archicortex; DMN, dorsomedial nucleus of the thalamus; EN, entorhinal cortex; FC, frontal cortex; HP, hippocampus; NC, neocortex; OB, olfactory bulb; PA, paleocortex; PY, pyriform cortex. (Modified from Lynch, 1990).

ably produces a more sophisticated motor control for performing complex movements with the jaws and limbs, and may also be associated with an increased somatosensory sensitivity.

In summary, in mammals the sensory and motor projections to the tectum which are characteristic of reptiles and amphibians were in large part shifted to the cerebral cortex via the thalamus, with the simultaneous reduction of the tectum. This may have largely been a consequence of reduction of the visual system and increasing olfactory development, with an expansion of the olfactory cortex and the consequent growth of neocortical areas receiving olfactory projections. Furthermore, the neocortex may have grown by virtue of increasing associative connections between olfactory projections and thalamocortical sensory projections (somatosensory, auditory and visual). The cerebral cortex also began to be involved in the control of complex motor actions, with the concomitant development of close associations with the motor systems of the brain.

All this process was accompanied by a dramatic increase in the size of the brain, produced as a consequence of the expansion of the neocortex (thalamo-telencephalic projections), and related to the elaboration of cognitive abilities (Jerison, 1973). However, the origin of the neocortex was not a direct consequence of selection for higher cognitive capacities, but rather resulted from adaptations to specific circumstances (reduction of the visual system and olfactory driven behavior). In other words, although the larger brain size of mammals may be related to an increase in cognitive capacities over reptiles, the fact that the particular structure that increased its size and complexity was the cerebral cortex was entirely circumstantial. (Birds increased their brain size and developed their cognitive abilities to a level comparable to mammals by using a different strategy.)

#### *An irreversible shift of functions*

I propose that at this point the cerebral cortex of mammals replaced the reduced tectum in many of its perceptual, integratory and motor functions. Perhaps the development of close links between the neocortex and the motor

systems in the brainstem was a key step in this replacement. This proposal is consistent with the concept of redundancy (degeneracy) in neural systems, where several neuronal populations located in different anatomical structures, may be capable of performing a certain function (Edelman, 1987). In this view, most neural functions are not strictly localized in a given brain region, but are susceptible to be performed in other anatomical loci as well. Although it may be difficult at this point to ascertain the specific functions that were replaced (Ingle, 1973; Stein and Gathier, 1981), I must note that both the optic tectum and the cerebral cortex, being laminar structures, are especially well suited for the establishment of high-resolution two-dimensional maps of neural projections (Edelman, 1987; Allman, 1990).

After the decline of reptiles, mammals underwent a major adaptive radiation. They reinvaded the diurnal niches, redeveloped their visual systems and the olfactory system became diminished in relative importance (Stephan *et al.*, 1970; Stephan, 1983). However, the optic tectum did not redevelop accordingly. It remained small and the thalamocortical system continued receiving the main sensory projections and controlling complex behavior. In other words, the shift of functions from the tectum to the thalamocortical system that had occurred previously turned out to be irreversible in this case. I have stated elsewhere (Aboitiz, 1989) that regressing organs that lose their function or whose function is taken by other organs are likely to be irreversibly lost. An extreme case of this situation is the well-known case of the irreversible loss of gills in tetrapods. Even when some tetrapods returned to live in water, they never reacquired gills because these were not functional in the moment of the reinvasion. In other words, when the historical path is reversed, the function originally played by the atrophied organ will either be played by some other organ or will not exist. In this case, selection will tend to act on a functional organ that performs a similar function, while the original organ will remain reduced.

The evolutionary history of the mammalian superior colliculus (optic tectum) seems to fit this pattern. After the reduction of the optic

tectum and the development of the olfactory system, many perceptual and motor functions residing mainly in the optic tectum begun to be performed in the cerebral cortex. Two key steps in this process were probably (i) the development of sensory associations between olfaction and the other senses in the hippocampus and some neocortical areas, and (ii) the elaboration of motor control by the neocortex, that permitted the performance of complex, learned motor actions. When mammals became diurnal again, the cerebral cortex was so involved in perception and motor command that the simpler strategy was to modify this working system instead of rebuilding the old visual system.

#### *The further evolution of neocortex*

I have proposed (Aboitiz, 1988) that the growth of the mammalian cerebral cortex favored the development of multiple cortico-cortical mapping systems that provide special properties to the brains of some mammals, especially primates (see Edelman, 1987). The cerebral cortex may have been especially well suited for the elaboration of these multiple projections by virtue of its laminar structure (Allman, 1990).

The evolutionary growth of the neocortex has been associated with an increase in neuroblast proliferation, resulting in an increased number of cortical cells (Rakic, 1988). This increase in cell number is mainly related to the addition of cortical columns (Rakic, 1988). However, across species the number of neurons increases at a slower rate than brain size (Jerison, 1973), thus increasing the relative size of the neuropil as brains grow larger. This results in an increased space for synaptic terminals. Furthermore, in phylogeny the cerebral cortex grows at a much faster rate than any other brain structure, accounting for most of the increase in brain size (Hofman, 1990). This produces an increase in cortical volume (mainly an increase in cortical surface) that is not matched by subcortical structures. Consequently, subcortical afferents to the expanded cerebral cortex find an excess of space to make synapses on. On the other hand, the cortical efferent system (mainly the projection to the basal ganglia and reticular forma-

tion) may overcrowd its subcortical targets by virtue of its growth.

In the perinatal period, there is an extensive process of retraction of axon collaterals in the cerebral cortex, based in large part on the competition for synaptic targets (Cowan *et al.*, 1984; Purves and Lichtman, 1985; Innocenti, 1986). This dramatically restricts the exuberant cortical connections of the newborn into the adult pattern. I suggest that in an expanded cerebral cortex, descending cortical projections (to basal ganglia and reticular formation) tend to suffer an extensive retraction of terminals, due to the overcrowding of their subcortical targets. On the other hand, many of these cortical efferents have been found to send collaterals back to the cerebral cortex both in the newborn and the adult (Stanfield *et al.*, 1982; Fisher *et al.*, 1986). In an expanded cerebral cortex, these recurring collaterals may find an excess of space to make synapses on and have a better probability of becoming stabilized. The net result of this hypothetical process would be an increase in the proportions of cortico-cortical projections that become stabilized, at the expense of cortico-subcortical efferents (Aboitiz, 1988). This may be a starting point for the development of complex cortico-cortical mapping systems that may result in increased cognitive capacities (Edelman, 1987).

Considering the evolution of the human brain, Geschwind (1964) argued that in man, the cerebral cortex would become more independent of subcortical structures by virtue of increasing the relative extent of cortico-cortical connections. Besides proposing a developmental mechanism for this process, I suggest that this phenomenon occurs not only in the evolution of the human brain, but as a general epigenetic consequence of the increase in the cerebral cortex in relation to subcortical structures. This phenomenon is most dramatic in man, but occurs as well in other cases of increase of cortical size and complexity.

I must emphasize that these multiple cortico-cortical projection systems may have become significant only late in the history of mammals, especially in animals such as primates, elephants and dolphins, and may have not been related to the origin and early evolution of the mammalian cortex.

### *The case for reptiles and birds*

In reptiles on the other hand (Fig. 1B), the cerebral cortex remained relatively small, since olfaction was not as developed as in mammals. Although not as dramatically as in mammals, the reptilian brain increased in size in the mesozoic period (Hopson, 1979), and presumably this was also related to an increase in thalamic projections to the forebrain. However, the brain structure receiving these thalamic projections (DVR) acquired a nuclear architecture, possibly due to the limited development of the cerebral cortex and because the ascending projections tended to be non-topographic or very coarse-grained (Ulinski, 1983). Also, neither the cerebral cortex or the DVR acquired the degree of motor control that is characteristic of mammals: these systems never project below the basal ganglia (Ulinski, 1983).

Birds (Fig. 1C) inherited the DVR of reptiles, which although more developed, retains its nuclear character. The size of the bird brain increased to reach mammalian levels, and a telencephalic laminar structure (the Wulst) appeared, while the optic tectum remained an important laminar structure in the brain. The lamination and relative importance of the Wulst are modest when compared to the mammalian cerebral cortex. This fact added to the poor olfactory sense of birds (as compared to primitive mammals) may explain the high development of the avian tectum. However, increased motor control by the telencephalon of birds has developed: the Wulst and the archistriatum send some descending projections to the brainstem, and the cerebellum has stronger connections with the telencephalon than in the case of reptiles (Ulinski, 1990b; Ulinski and Margoliash, 1990; Rehkämper and Zilles, 1991). Additionally, birds have projections from the basal ganglia to the thalamus that seem to be intermediate in terms of development between reptiles and mammals (Brauth, 1990).

Thus, although there was a telencephalic increase in reptiles and birds, and there are many common themes between the telencephali of reptiles and birds and mammals, the difference exists in terms of the growth of the mammalian neocortex at the expense of the size of the optic tectum. In

reptiles and birds (especially the latter), telencephalic expansion was concomitant with the expansion of the tectum (Ulinski and Margoliash, 1990) because these two structures were not competing for the performance of perceptual, integratory and motor functions as they were doing in mammals.

A situation more similar to mammals is the special case of ophidians and some nocturnal lizards. Snakes are derived from fossorial reptiles whose visual system became atrophied (Walls, 1942). In ophidians, the tectum is reduced and the visual projections are somewhat shifted to the thalamus (Ulinski, 1971, 1977). Furthermore, as in mammals, there are no basal ganglia projections to the tectum via the pretectum (Medina and Smeets, 1991). However, the reduction of the tectum is not as dramatic as it is in mammals, and in snakes it may have reexpanded after reinvasion of the surface. I suggest that, since ophidian ancestors had developed a nuclear dorsal ventricular ridge and a relatively small cortex, the functions performed by the laminar optic tectum could not be easily performed in the anterior brain (*i.e.*, cortex and DVR). In addition reptiles did not develop olfaction as mammals did, and there was no opportunity to develop the cerebral cortex, even if the tectum was reduced. This situation may have constrained the reduction of the optic tectum in nocturnal and fossorial reptiles, since there were no structures replacing its functions as the cerebral cortex was doing in mammals. In this way, the reduction of the tectum was a reversible phenomenon in the history of ophidians.

### *Homology or analogy between neocortex and DVR?*

The question of the homology between mammalian neocortex and DVR is far from being solved. Although there are important common themes in terms of connectivity and function (Ulinski, 1983; Reiner, 1991), it is not clear whether the two structures represent the same embryonic cell group or not. It has been proposed that some cortical areas (including visual extrastriate, inferotemporal and auditory cortices) arose as a tangential migration of neuroblasts from the DVR (Nauta and Karten, 1970; Karten and Shimizu, 1989;

Karten, 1991). This hypothesis has been challenged (Ulinski, 1986) on the basis of the absence of embryological evidence for (i) a proliferative zone ventral to the pallium, and (ii) a tangential migration of neuroblasts in the embryonic cerebral cortex. However, some findings do point to a possible proliferative zone in the lateral ventricle of the rabbit (Stensaas and Gilson, 1972), and a recent report opens the possibility of tangential migration of neuroblasts in the cerebral cortex (Walsh and Cepko, 1992; however, the results do not seem consistent with a massive migration of neuroblasts from the lateral ventricle towards its dorsal and medial portions). Therefore, this body of evidence so far does not conclusively support either view.

A different kind of evidence seems to support the non-homology hypothesis. First, paleoneurological analyses suggest that pelycosaurs and mammal-like reptiles had very elongated, tubular hemispheres and consequently lacked a DVR (Hopson, 1979; Ulinski, 1986). Therefore the lineage of mammals may have never had a DVR. If this is correct, DVR would be better thought of as a derived structure of reptiles and birds, rather than an ancestral feature of amniotes.

A second source of evidence is the different topographic localization of the neocortex and DVR in the cerebral hemispheres. It has been suggested that DVR originates between the dorsal and lateral cortices of reptiles (which roughly correspond to neocortex and paleocortex of mammals; Quiroga, 1980). However, a more conservative approach is that DVR arises in a more ventral position, adjacent to the basal ganglia in the embryonic hemisphere (Nauta and Karten, 1970; Karten and Shimizu, 1989). This situation is very clear in reptiles with a small DVR (see Ulinski, 1990b). Therefore, in the primitive condition, lateral cortex (paleocortex of mammals) lies between dorsal cortex (neocortex of mammals) and DVR. For the tangential cell migration hypothesis to be correct, neuroblasts would have had to cross lateral cortex (paleocortex) before reaching the neocortex, which makes the mechanism perhaps too complicated, especially if an ancestral DVR never existed in the lineage that led to mammals.

In this context, the important evolutionary question regarding DVR is not its comparison with mammalian neocortex, but its origin from an ancestral brain similar to that of amphibians. It is paradoxical that most studies attempting to homologize DVR with other vertebrate brain structures have been done comparing avian and mammalian brains (Nauta and Karten, 1970; Karten and Shimizu, 1989; Rehkämper and Zilles, 1991). Based on its connectional and histochemical similarities with mammalian neocortex, DVR is now considered to be related to the dorsal part of the hemisphere (pallium), rather than to its ventral part (subpallium). MacLean (1986) has recently revived an argument for the homology of DVR with the mammalian claustrum, a hypothesis that would be consistent with the view presented here. Another hint to the origin of DVR is its possible embryonic relation with the prosomeres of the anterior brain (Karten, 1991).

If neocortex and DVR represent different embryonic cell groups (my personal bias), this would indicate that thalamic nuclei projected to different brain regions in reptiles and mammals, and these regions subsequently acquired specific architectonic patterns (nuclear or laminar). If, on the other hand, neocortex and DVR represent the same embryological cell group, this would indicate that this same brain region acquired different architectures in reptiles and mammals, depending on the relations with other brain structures.

#### FINAL COMMENT

The scenario I am depicting for mammalian brain evolution is a succession of adaptations whose combination was to a large extent fortuitous, which led to the mammalian plan of brain organization. The adaptation to nocturnal life, along with the elaboration of the olfactory system, brought about irreversible changes in the structure of the brain. Some of these adaptations were paralleled in reptiles such as snakes, but these did not occur in the combination required to produce an irreversible change in structure. As a result of historical circumstances, the optic tectum was reduced in mammals while increasing in size in birds, and on the other hand thalamic sen-

sory projections were directed to a laminar structure (neocortex) in mammals and to a nuclear structure (DVR) in reptiles and birds. This hypothesis is consistent with the concept of evolutionary innovations resulting from contingent processes of adaptation, which in specific circumstances may result in major changes in structure. This approach differs from a perspective that views the evolutionary origin of the neocortex as a step in a progressive series towards increased intelligence (Papez, 1929; Jackson, 1931; Ariens Käppers *et al.*, 1936; Brown, 1967, 1991; MacLean, 1973; Foskett, 1978; Aronson, 1984; Yarczower, 1984; Glezer *et al.*, 1988; for critical reviews, see Walker, 1983; Deacon, 1990a, b). I propose that only later, in some mammals did the cerebral cortex play a significant role in increasing cognitive capacity, with the development of multiple corticocortical projection systems.

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