

# Evolutionary origins of the reptilian brain: The question of putative homologues of dorsal ventricular ridge. An overview and proposal\*

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*The reptilian brain is characterized by a structure that bulges into the lateral ventricle, called dorsal ventricular ridge (DVR). The DVR was originally considered to be a part of the basal ganglia, although more recent studies indicate that it may correspond to the dorsal part of the hemisphere. The anterior portion of the DVR has several connectional and functional similarities with parts of the mammalian neocortex, for which reason it has been claimed that the two structures can be considered as homologues. In this article I review the evidence supporting and refuting homology of the DVR with different telencephalic structures of mammals, concluding that it is still early to unequivocally ascribe structural correspondences between the different components in the two vertebrate classes. However, a way out of the problem is suggested by comparing the embryonic position of DVR with that of lateral cortex in the reptilian hemisphere. The lateral cortex is considered to be quite comparable in reptiles and mammals, and hence may be a good marker for the original position of the DVR. If the DVR originates dorsal to lateral cortex, it may be considered comparable to parts of the mammalian neocortex, while if it develops in its same position or ventral to it, it may not correspond to the neocortex. Early embryological work indicated that the DVR develops in the same position as the lateral cortex, but arises as a late migration wave, after cells destined to lateral cortex are generated. In other words, instead of being interposed between dorsal and lateral cortices, the DVR may originate in a position overlapping with lateral cortex. If this alternative turns out to be the case, it may imply that the DVR arose *de novo*, through an extension of the ancestral period of neuroblast proliferation. As a consequence, there may be no structures comparable to it in other vertebrate classes. Finally, it is also proposed that, regardless of whether the DVR and the extrastriate neocortex can or cannot be considered phylogenetic homologues, some of the integrative functions performed by them might have a common evolutionary origin, that became localized in the reptilian DVR and in the mammalian extrastriate neocortex.*

**Key words:** dorsal ventricular ridge, homology, lateral cortex, reptiles, telencephalon.

\* Some of the issues presented in this paper are discussed at full length in Aboitiz (1995a).

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## ABBREVIATIONS

b	Ventricular zone b
D	Dorsal pallium
DVR	Dorsal ventricular ridge, anterior component
DLVR	Dorsolateral ventricular ridge
L	Lateral pallium
Lat	Lateral
LG	Lateral ganglionic eminence
M	Medial pallium
Med	Medial
MG	Medial ganglionic eminence
PT	Pallial thickening
St	Striatum
SVZ	Subventricular zone
VZ	Ventricular zone
V	Lateral ventricle

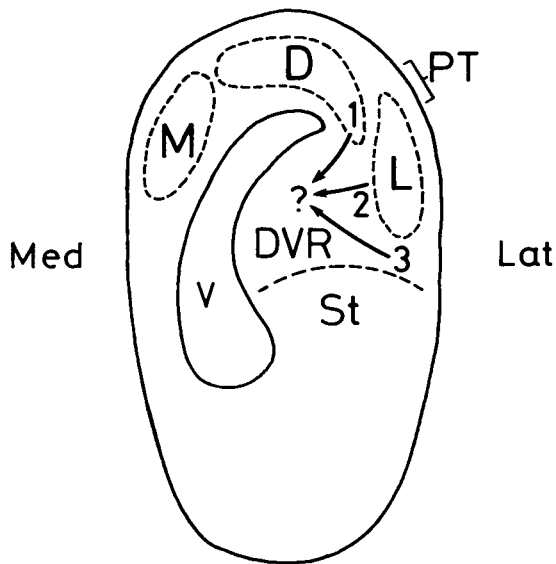
## INTRODUCTION

In previous articles, I have suggested evolutionary scenarios for the origin and development of the mammalian neocortex (Aboitiz, 1992, 1993). A problem that has remained open in these reports is the possible homologue of the mammalian neocortex in the reptilian brain. In mammals, although there is great expansion of the telencephalic wall with the origin of neocortex, there has been no major distortion of the ancestral topographic plan in the hemisphere. In reptiles however, the situation is complicated because there is a structure known as the dorsal ventricular ridge that instead of developing outwards, bulges into the ventricular space, distorting the topographic relations between the different telencephalic components (Ulinski, 1983). Moreover, the anterior moiety of the dorsal ventricular ridge (this moiety will hereafter be designated as DVR) shares many characteristics with parts of mammalian neocortex, such as receiving visual projections from the retino-tectothalamo-telencephalic path (the tectofugal path), and also receiving auditory and somatosensory projections. Based on these findings, it has been suggested several times that the DVR is an evolutionary homologue of the extrastriate visual areas and other neocortical areas, mammalian cortex having derived from a DVR-like structure.

The correspondence of the DVR with telencephalic structures in other vertebrates is essential for understanding the evolutionary origin of the brain of reptiles (and birds), as any possible scenarios are constrained by the locus of origin of this component. In fact, we will see that the subject of determining homologues of the DVR in other vertebrates -especially mammals- is nowadays a matter of intense debate. In this article, I will review the evidence favouring and against the possible homology between the mammalian neocortex and the reptilian DVR, and conclude that there is still little evidence to support or refute an homology hypothesis. However, I will suggest the use of an anatomical marker such as the position of lateral cortex as a good criterion to establish homology.

## DVR VS MAMMALIAN NEOCORTEX

The DVR is a nuclear, non-laminated component of the telencephalon of reptiles that bulges into the lateral ventricles (Fig 1). Its anterior portion receives projections from the tectofugal visual pathway, from auditory and from the somatosensory modalities. In the adult, this region is adjacent and dorsal to the corpus striatum, and was originally thought to be a modified part of the basal ganglia, designated as the "hypopallium" by Elliot Smith (1919), who considered that both the DVR and the corpus striatum were cortical in origin. Johnston (1923), Holmgren (1925) and Cairney (1926) also argued for the DVR as a structure derived from the basal ganglia. The non-striatal nature of the DVR was indirectly suggested by hodological studies that demonstrated ascending sensory projections to this structure (Karten, 1968, 1969; Karten and Hodos, 1970); and later it was established by immunocytochemical studies that determined the limits of the corpus striatum by the presence of the enzyme acetylcholinesterase (Parent and Olivier, 1970; Parent, 1986). Ulinski (1983) proposed that during embryogenesis, the middle ventricular sulcus separated the corpus striatum ventrally and the DVR dorsally, thus supporting the concept of the DVR as a structure unrelated to the corpus



**Fig 1.** Possible embryonic positions of DVR in the reptilian hemisphere, as seen in a diagram of a transverse section. 1, Reiner (1993) and Butler (1994b) among others argue that it is originally located between dorsal and lateral cortex. 2, Källén (1951), Ulinski (1983) and others argue for an origin related to lateral cortex. 3, Yanes *et al* (1987, 1989) and Lohman and Smeets (1990) claim an origin for DVR that is ventral to lateral cortex. If it corresponds to the same embryonic anlagen as lateral cortex or is originated ventral to it, it may not be embryologically comparable to neocortex. D, dorsal pallium (cortex); L, lateral pallium (cortex); Lat, lateral; M, medial pallium (cortex); Med, medial; PT, pallial thickening; St, striatum.

striatum. In birds, the DVR develops into the ectostriatum, neostriatum and hyperstriatum (Nauta and Karten, 1970; Ulinski, 1983; Karten and Shimizu, 1989; Karten, 1991; Shimizu and Karten, 1991a, b; Rehkämper and Zilles, 1991).

Nauta and Karten (1970), Karten and Shimizu (1989), Karten (1991), and Shimizu and Karten (1991a, b) argued that despite their architectural differences, the DVR of birds was comparable to the extrastriate neocortex of mammals. Based on the striking connectional similarities between these two structures, they proposed the "equivalent cell hypothesis", which suggested a shared circuit ancestral to birds and mammals (and hence reptiles). This neural circuit successively included the tectum, thalamus, ecto-, neo- and archistriatum in the case of birds; and the tectum, thalamus, and cortical layers IV, II-III, and V-VI in the case of mammals. However, further considerations now suggest

that this hypothesis may not be correct. Hodological and neurochemical evidence indicates that neocortical layers II, III and IV arose as new structures in the origin of mammals since the connections and/or cell types present in these layers are absent from the reptilian cortex and the DVR (Ebner, 1976; Reiner, 1991, 1993). Furthermore, superficial neocortical layers are the latest to be generated in development (Goffinet, 1983), suggesting that they arose through an extension of the ancestral period of neuroblast proliferation. Therefore, it is more likely that the above mentioned circuits arose separately in the two vertebrate classes. Recent studies now indicate that mammalian isocortex does not derive from a DVR-like structure as Karten and collaborators implied. Rather, the DVR can be viewed as a derived character of reptiles (and birds), while the neocortex is a derived character of mammals (Aboitiz, 1992, 1993; Reiner, 1993; Butler, 1994a, b). However, these two structures might still derive from a common primordial anlage that diverged into different neural architectures in the two classes (reptiles and mammals).

In agreement with Elliot Smith (1919), Senn (1979) and Ulinski (1991) depict the reptilian DVR as a structure located ventral to lateral (olfactory) cortex, and dorsally adjacent to the corpus striatum (see Fig 1), a position that contrasts with the position of the mammalian neocortex, which is undoubtedly dorsal to lateral cortex. Based on this evidence, and on the embryological work of Yanes *et al* (1987) and the interpretation of Lohman and Smeets (1990), describing the embryonic precursor of the DVR as a sub-cortical structure, I considered that the neocortex and the DVR were not derived from the same embryonic cell group (Aboitiz, 1992, 1993). Supporting this view, the anatomical description of Yanes *et al* (1989) and a recent immunocytochemical study by Andreu *et al* (1994) indicate that DVR is in a position adjacent to the corpus striatum. However, adult topographic position may result from distortions of the original embryological plan, and thus may not adequately reflect the spatial relations between developing structures.

Early embryological work on snakes (Warner, 1946), lizards (Hetzel, 1974),

*Sphenodon* (Hines, 1923), crocodiles (Källén, 1951) and turtles (Holmgren, 1925; Källén, 1951; and Kirsche, 1972) implied that the DVR emerges from a position equivalent to lateral cortex in the hemisphere (Fig 1), but arises as a late migration wave, after the migration of cells belonging to lateral cortex. Later in development, the DVR bulges into the ventricle and in many cases shifts its relative position towards one ventral to lateral cortex and immediately dorsal to the corpus striatum (see Ulinski, 1983). In birds, who do not have a well-developed lateral cortex, the DVR does not protrude in the ventricle (that remains as a small structure) but grows lateralward (Ulinski, 1983). Although it is seldom (if ever) stated explicitly, this developmental perspective supports the concept of non-homology between the DVR and the neocortex, since the two structures apparently have different embryological origins.

At least two recent papers (Reiner, 1993; Butler, 1994b) literally turned around this issue by proposing a topographic position of the DVR in the hemisphere that is equivalent to extrastriate neocortex. Reiner (1993) argues that in primitive reptiles the DVR is continuous with the dorsal cortex. In turtles, this continuity may take place through the pallial thickening, which is a region of cellular discontinuity between the lateral and the dorsal cortices (see Fig 1), while in *Sphenodon* dorsal cortex is supposed to continue around the lateral ventricle into the DVR. To Reiner, this implies a topographic location of the DVR comparable with that of the extrastriate isocortex, that is, between dorsal and lateral cortices. However, cellular continuity through the pallial thickening does not necessarily imply that the DVR is interposed between dorsal and lateral cortices; this continuity may also be expected if the DVR arises in the same position as lateral cortex, as indicated by embryological studies. Furthermore, in their diagrams of the telencephalon of *Sphenodon*, Senn (1979) and Ulinski (1990) place the lateral cortex just between the dorsal cortex and the DVR, indicating that the latter is located ventral to lateral cortex.

Butler (1994b) suggests homology between the DVR and neocortex on the basis

of the existence of a subventricular zone (SVZ) in the two structures during development. The SVZ is an embryonic proliferating layer superficial to the ventricular zone. It has been proposed that its contribution is mainly glial, as opposed to the ventricular zone that produces mostly neurons (Nowakowski and Rakic, 1979; Miller, 1988; Bayer and Altman, 1991). (Nevertheless, at least in its anterior portion, the SVZ has been found to be the source of neurons that migrate tangentially to the olfactory bulb [Luskin, 1993].) Butler (1994b) refers to the work by Smart and Smart (1977) in mammalian embryos, describing the SVZ mostly in the lateral and medial ganglionic eminences (Fig 2), but not in the dorsomedial cortex (that may give rise to the striate cortex). According to these authors, in the lateral and medial eminences the SVZ respectively gives rise to the lateral (extrastriate) neocortex, and to the olfactory tubercle, pyriform cortex and the striatum. In reptiles, Butler cites the embryological work of Yanes *et al* (1987), describing the DVR as emerging from a ventricular area called zone b (Fig 2). Apparently, the SVZ is present in zone b but not in dorsal cortex (Goffinet, 1983). Therefore, by virtue of sharing a SVZ, zone b of reptiles might be comparable to the lateral and medial ganglionic eminences of mammals, and hence their final products, the DVR and extrastriate neocortex might develop from the same embryonic anlagen. (There is also another proliferative region dorsal to zone b that also bears a SVZ, the sulcus lateralis [SL] that has been described as contributing to dorsal cortex in some reptiles but to DVR in some others such as lizards [Webster, 1973], and has been proposed by Karten [1991] to give rise to the dorsolateral ventricular ridge [Fig 2].)

In spite of the above, there is a different interpretation of the fate of the medial and lateral ganglionic eminences of mammals. Recent embryological work (Bulfone *et al*, 1991; Puelles and Rubinstein, 1993; O'Rahilly and Müller, 1994) asserts that they give rise to subcortical structures- especially the corpus striatum. Furthermore, the absence of a SVZ in embryonic dorsomedial cortex may be questionable. Bayer and Altman (1991) indicate that the SVZ

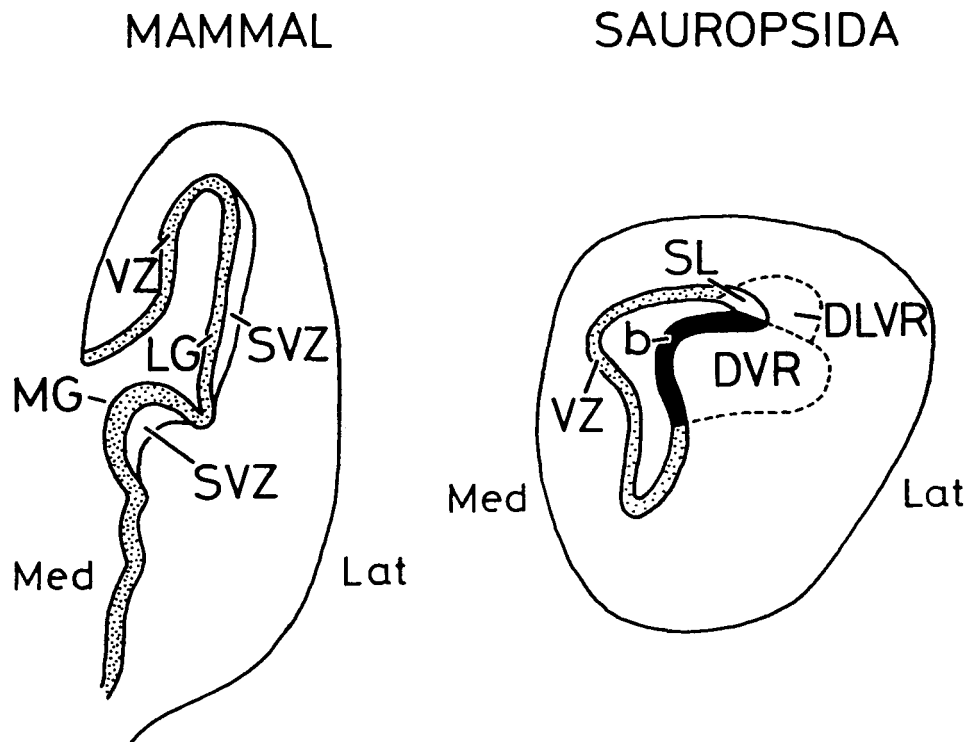


Fig 2. A. The position of the lateral and medial ganglionic eminences (LG, MG), bearing ventricular (VZ) and subventricular (SVZ) zones in a transverse section of the embryonic hemisphere of a mouse. B. Butler (1994b) compares the position of the ganglionic eminences to that of dorsal ventricular ridge (DVR) emerging from ventricular zone b (b), and to the dorsolateral ventricular ridge (DLVR) emerging from the sulcus lateralis zone (SL) in the embryonic hemisphere of sauropsida (reptiles and birds). Data from Yanes *et al* (1987) and Butler (1994b). Lat, lateral; Med, medial

emerges ventrolaterally in the hemisphere, and grows to the dorsomedial moiety later in development, following the same generative gradient as the rest of the hemisphere. Therefore, in the study of Smart and Smart (1977) the presumed absence of a SVZ in the dorsomedial part of the hemisphere may perhaps be a consequence of the use of early embryonic material in which the SVZ has not yet developed in the dorsal region. The contribution of the SVZ to cortical development is still unresolved, and the evidence indicates that in mammals there may be several structures bearing an embryonic SVZ (Miller, 1988; Bulfone *et al*, 1991; Luskin, 1994), implying that the neocortex is not the only candidate for homology with the DVR according to this criterion. In this context, Karten and Shimizu (1989) argue that the embryonic equivalent of the DVR in mammals might be located in a proliferative zone found in the lateral

ventricle of the rabbit (Stensaas and Gilson, 1972), although there is not much evidence in their support.

#### PROPOSALS

Thus, the embryological origin of the DVR and its possible mammalian counterpart are largely unsolved problems. In mammals, the position of the neocortex clearly indicates an origin dorsal to the lateral cortex, and its location implies no major topographical transformation of the ancestral plan of the hemisphere (Aboitiz, 1992, 1993). In reptiles, the situation is more confusing as the ancestral plan appears distorted because of inward bulging of the DVR into the ventricle (Ulinski, 1983; Reiner, 1993; Kirsche and Kirsche, 1993), as opposed to the outward migration of cortical structures. In this context, the use of a landmark will be very

helpful in determining the embryonic position of the DVR in relation to other hemispheric structures. I propose that the lateral cortex may be considered as such a landmark, since its position and borders are well established at least for mammals and amphibians (Ariens Käppers *et al*, 1936; Herrick, 1948; Ulinski, 1990). Although early scholars did pay attention to the embryonic relations between the lateral cortex and the DVR, the former structure is notably absent in more recent discussions of homology. The lateral cortex appears in different positions relative to the DVR in the diagrams of different workers (according to their respective views on the subject), but these authors barely mention its relations with the DVR as a criterion for homology.

In order to be embryologically comparable to some neocortical areas, the DVR should originate dorsal to lateral cortex. If it is found ventral to it, it is then a subcortical structure, perhaps related to components such as the claustrum (McLean, 1986). The third and to me, most interesting alternative is that the DVR and the lateral cortex arise *in the same topographic position in the hemisphere, one external to the other*. That is, instead of being interposed between different cortical components as modern authors imply, the DVR might originate from a region that overlaps with some of them (especially lateral cortex). As said, Källén (1951), Ulinski (1983) and others already proposed that the pyriform (lateral) cortex and the DVR were generated in the same proliferative zone in the telencephalon, with pyriform cortex being generated first and then pushed lateroventrally by the DVR, which differentiated in situ in the lateral wall of the hemisphere. If this turns out to be the case, although establishing a pallial origin for the DVR, it would indicate that the DVR and the mammalian neocortex are embryologically not comparable (unless either a similar embryonic origin for extrastriate cortex is found, or that cells originally dorsal to the lateral cortex underwent a massive ventral migration in the origin of the reptilian DVR).

In relation to the third possibility, the DVR may be a genuine novelty in the evolution of the reptilian brain; that is, its

constituent cells may have been acquired *de novo*, by an extension of the period of embryonic neuroblast proliferation in the telencephalic wall. As mentioned, a similar case is probably found in the origin of supragranular layers of the mammalian neocortex (Reiner, 1991), where these phylogenetically new structures are the latest-generated cortical cell groups. If this view is correct, it makes no sense to look for structures ancestral to the DVR. Furthermore, if as stated above the DVR is a derived character of reptiles, then the concept of homology between this structure and mammalian neocortex becomes questionable.

A promising approach to study the comparative aspects of hemisphere components is the expression of homeotic and homeotic-like genes during early telencephalic development. A positional pattern of gene expression similar to that originally described in the hindbrain has been recently found in the diencephalon and telencephalon, which also corresponds to the segmented pattern of the anterior neural tube (Bulfone *et al*, 1991; Figdor and Stern, 1993; Puelles and Rubinstein, 1993). A topographic matrix determining the position of each segment and its components has been proposed, where each compartment is defined by a unique combination of expressed homeotic genes. Although the patterns and arrangements proposed may not be definitive as yet, eventually and with hope they may offer clear markers of specific embryonic regions in the cerebral hemispheres and perhaps also the thalamus. In this context, we may recall that Karten (1991) proposed that the DVR develops from a specific telencephalic segment, the DVR prosomere, which according to Butler (1994b) corresponds to Yanes *et al*'s (1987) zone b. It remains to be seen how this putative prosomere fits the segmental pattern of Bulfone *et al* (1991) and Puelles and Rubinstein (1993).

In spite of the above, there are also some caveats to be made regarding this approach: it has been found that some cranial nerve nuclei may shift their segmental position in phylogeny (Gilland and Baker, 1993). In more advanced vertebrates, there is a compression of the motor nuclei of the brainstem into progressively more rostral

neuromeres. Furthermore, if the interpretation of Butler (1994a) on the phylogenetic rearrangements of thalamic nuclei is correct, a similar situation may occur in the thalamus, indicating that the phenomenon is not uncommon. In the same line, De Beer (1971) argued that vertebrate limbs, although having a common ancestry, do not stem from equivalent body segments in all vertebrates. In this way, although a common pattern of early gene expression may be found for the cerebral hemispheres in different vertebrate classes, neuronal groups may shift their segmental positions during phylogeny. Therefore, perhaps the criterion of relative embryonic position is stronger than the allocation of a cell group to a specific embryonic segment.

#### DISCUSSION

The evidence reviewed indicates that in the comparative study of the DVR and the neocortex, the different criteria for homology yield contradictory results. Supporting the hypothesis of homology, Karten (1991) relies mainly on connectional and functional criteria, while Reiner (1993) relies on immunocytochemical markers (the DVR shares neurochemical markers with reptilian dorsal cortex) but more on indicators of relative position in the hemisphere. Butler (1994b) bases her views mainly on embryological evidence. On the other hand, the perspectives of Ulinski (1990) and Senn (1979), based on relative position, and those of Källén (1951), Ulinski (1983) and others based on embryonic studies, argue for non-homology. At first sight it is difficult to see how this controversy will have an end.

Assuming that the embryonic topography of major hemispheric components is a highly conserved character, and that the ventral border of cortical or cortical-like structures is given by the ventral border of lateral (olfactory) cortex, I suggest that the criterion of embryonic position is at this point the most reliable criterion to establish whether there is phylogenetic homology between the reptilian DVR and the mammalian neocortex (for a full-length discussion, see Aboitiz, 1995a). A position of the DVR dorsal to the

lateral cortex would imply homology with the neocortex, while a different position would need evidence of a massive cell migration to assume homology. Another aspect of interest is to compare the timing of neuronal incorporation into the DVR and into lateral and medial cortex in reptiles. If the DVR is found to develop by an extended period of neural proliferation in the region corresponding to the lateral cortex, it may not have ancestral structures and hence a comparison with the mammalian isocortex is meaningless. Connectional and neurochemical evidence may not be considered as fundamental in determining homology, since -for example- connections are known to have shifted in telencephalic evolution from striatal auditory connections to cortical ones in amphibians (Frost and Masterton, 1992), and geniculate visual projections are known to shift their targets widely in reptiles (Shimizu and Karten, 1991a). Transmitter characteristics may perhaps be a consequence of the connectional and functional relations of the cell groups, thus shifting neurotransmitters according to changes in connections. A related approach to the problem is the study of patterns of homeotic-like gene expression, that may provide a matrix of positional relations between embryonic components of the hemisphere in the same way as they do in the embryonic hindbrain. However, it should be recalled that there is evidence that some hindbrain and midbrain nuclei have been displaced across segments in phylogeny, therefore complicating the relations between embryonic segments and adult cell groups.

The DVR in reptiles may have developed concomitant with the increase in brain size associated to the origin of reptiles (Northcutt, 1981), in much the same way as the mammalian neocortex developed associated with an increase in encephalization during the origin of mammals. I proposed here that the DVR, as well as the supragranular layers of neocortex (the key innovation in neocortical origins; Reiner, 1991) might have arisen as *de novo* structures, through an extension of the period of neuroblast proliferation. Associated to the colonization of land, there may have been strong selection for more refined perceptual, motor and

integrative representations, which were probably facilitated by an increase in size of the respective brain regions (Aboitiz, 1995b). In this context, the reptilian and the mammalian brains may have suffered great selective pressures for growth, that resulted in the origin of new structures for which there are no ancestral elements besides the general embryonic anlagen to which they belong.

It is worth mentioning at this point that Elliot Smith (1919) proposed that in reptiles the DVR shifted its original position by following the principle of neurobiotaxis, that consists of the migration of neural cells towards the source of their main afferents, in this case thalamic nuclei. In the development of mammalian neocortex, the late-generated, phylogenetically newer cells migrate across earlier-generated cells, becoming localized in a more external position than the latter (Goffinet, 1983). I (Aboitiz, 1993) suggested that this inverted lamination pattern evolved as a strategy that enabled the newer cortical cells to establish synaptic contacts with thalamic afferents that were primitively located in the more external layer I of the cortex. In this way, another parallelism may have occurred in the origin of reptilian DVR and in mammalian superficial neocortical layers, consisting of the displacement of the newly-generated cells towards their thalamic afferents. Different embryological and connectional circumstances resulted in two different solutions to the same problem: DVR was displaced medioventrally in reptiles, closer to the lateral forebrain bundle (that carries the thalamic afferents to the pallium), while in mammals cells of layers II-IV migrated across the phylogenetically older cells of layers V and VI to establish contact with thalamic terminals in layer I.

In the beginning, probably both the DVR and the neocortex performed integrative perceptual functions. The mammalian neocortex may have developed in a laminar fashion associated to the reduction of other laminar structures such as the optic tectum, that processed most topographic visual information. In this sense, the mammalian visual cortex may have functionally replaced the optic tectum (discussed in Aboitiz, 1992, 1993). In reptiles, and perhaps due to its

periventricular position, the DVR developed a nuclear, non-laminar architecture while most of the topographic information kept being processed in the optic tectum, which is the main laminar structure of the reptilian brain and projects to the DVR indirectly through the nucleus rotundus of the thalamus (Aboitiz, 1992, 1993).

Although the DVR and the neocortex might not have a common embryonic or evolutionary origin, I suggest that there still exists an argument for a common ancestry of some of the integrative functions performed in the DVR and in mammalian extrastriate neocortex. Phylogenetic homology need not be circumscribed at a single hierarchical or phenomenical level such as that of anatomy, but may be found at the level of developmental processes, functions and behavior (for a full discussion, see the classical work by Lorenz, 1965; and also Striedter and Northcutt, 1991; Lauder, 1994; and Aboitiz, 1995a). Some primordial telencephalic functions integrating different sensory modalities may have been performed in the brains of the common ancestors of reptiles and mammals. Originally, these functions may have been performed in some as yet undetermined part of the telencephalon and eventually they became localized (and progressively elaborated) in the reptilian DVR, in mammalian neocortex and in the striatum of present-day amphibians (Smeets and González, 1994; Butler, 1994a, b). Regardless of whether the DVR and neocortex are or not evolutionary homologues, some of these integrative functions may have been conserved in phylogeny despite their putative shifts in brain location. In other words, evolutionary homology of the DVR with extrastriate neocortex is not required for homology in their functions (see Striedter and Northcutt, 1991; Lauder, 1994; Aboitiz, 1995a).

Summarizing, this review critically discusses recent comparative work on the evolutionary origin of the DVR. Based on connectional, topographic and embryological evidence, the latest position papers argue for homology between the reptilian DVR and the mammalian neocortex (Karten, 1991; Reiner, 1993; Butler, 1994b). This review takes a different approach, highlighting early devel-



perimental work on the embryonic origins of the DVR, which has been largely neglected by other authors. These early studies indicated that the DVR overlaps spatially with lateral cortex during development, but emerges after the cells destined to the latter have migrated. If this interpretation is correct, it poses a serious problem to the concept of homology between the DVR and the neocortex.

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