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# Succinic Dehydrogenase Histochemistry Reveals the Location of the Putative Primary Visual and Auditory Areas within the Dorsal Ventricular Ridge of *Sphenodon punctatus*

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**Key Words**

Tuatara · Telencephalon · Basal ganglia · Reptiles · Histochemistry · Evolution

**Abstract**

In turtles, crocodilians, lizards and snakes, the dorsal ventricular ridge (DVR) is a nuclear cell mass that contains distinct visual and auditory thalamorecipient cell groups. In the tuatara *(Sphenodon punctatus),* the DVR is not organized into diverse cell groups but instead possesses a trilaminar cytoarchitecture resembling that characteristic of the telencephalic cortex in reptiles. To determine if visual and auditory fields might also be present in the DVR of *Sphenodon punctatus,* we used succinic dehydrogenase (SDH) histochemistry, which has been shown to delineate the visual and auditory fields of the DVR in turtles, crocodilians and lizards. We also used acetylcholinesterase (AChE) histochemistry to determine the boundary between the DVR and the basal ganglia in *Sphenodon*. We found an SDH-rich region in the neuropil ventral to the cell plate of the rostrolateral DVR and a slightly less intense SDH-rich zone in the neuropil deep to the cell plate of the ventromedial DVR. These SDH-rich zones appear to be located at the apical dendrites of the neurons of the adjacent cell plate. These SDH-rich zones were clearly located within the DVR and were distinct from the AChE-rich striatal part of the basal ganglia, which occupied the ventrolateral wall of the telencephalon. Based on findings in other reptiles, it seems likely that the SDH-rich zone in rostrolateral DVR represents the zone of termination of nucleus rotundus visual input to the DVR, whereas the zone in ventromedial DVR represents the zone of termination of nucleus reuniens auditory input. Because a trilaminar DVR such as that in *Sphenodon* might be the primitive DVR condition for reptiles, our results suggest that the cytoarchitecture of the DVR and the synaptic organization of its thalamic sensory input in the common ancestor of living reptiles might have been much like of the dorsal cortex.



## Introduction

The dorsal ventricular ridge (DVR) is a pallial expansion of the lateral telencephalic wall that is present in all living reptiles and birds (sauropsids) [Northcutt, 1978, 1981]. The DVR bulges into the lateral ventricle, and its anterior part has been shown to be largely sensory in function and its posterior part has been proposed to be largely amygdaloid in nature [Northcutt, 1981; Andreu et al., 1996; Lanuza et al., 1997, 1998; Guirado et al., 1999]. In all sauropsids except the lizard-like rhynchocephalian reptile, *Sphenodon punctatus*, the DVR consists of a field of separate nuclei of variable distinctness [Northcutt, 1978, 1981]. In turtles, crocodilians,

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lizards and birds, a distinct cellular field within the lateral part of the anterior DVR, just dorsal to the striatal part of the basal ganglia, receives input from a thalamic nucleus known as nucleus rotundus. In turtles this telencephalic field has been termed the core nucleus or dorsal nucleus [Johnston, 1915; Hall and Ebner, 1970a; Parent, 1976; Balaban and Ulinski, 1981]; in birds it has been termed the ectostriatum [Karten and Hodos, 1970]. In lizards and crocodilians, this region is typically called the rostrolateral or dorsolateral part of the DVR [Pritz, 1975, 1980; Bruce and Butler, 1984a, b]. In both turtles and birds, the neurons of this DVR cell group are large and multipolar, and the input from nucleus rotundus ends on their perikarya and dendrites. Nucleus rotundus itself receives visual input from the tectum in birds and reptiles [Karten and Revzin, 1966; Revzin and Karten, 1966; Hall and Ebner, 1970b; Foster and Hall, 1975; Pritz, 1975, 1980; Rainey and Ulinski, 1982; Reiner, 1994; Luksch et al., 1998]. Thus, the rotundal target within the DVR is visual, and electrophysiological and lesion studies have confirmed that it plays a prominent role in the visual behavior of reptiles and birds [Hodos and Karten, 1970; Reiner and Powers, 1980, 1983; Dunser et al., 1981; Bass et al., 1983]. Because the visual area within DVR is clearly distinct from the primary visual area in the Wulst of birds and in the dorsal cortex of turtles [Hall and Ebner, 1970a; Hall et al., 1977; Desan, 1988; Ulinski, 1988], and because this secondary telencephalic visual area receives visual input from a thalamic region that receives its visual input from the tectum, we will refer to the rotundorecipient visual area of the DVR as the tectothalamofugal visual area, or Vtt. The primary visual area in dorsal cortex and in the Wulst, which appears homologous to primary visual area 17 of mammalian neocortex, will be referred to as V1 [Karten, 1969, 1991; Nauta and Karten, 1970; Medina and Reiner, 1999].

In reptiles and birds, the anterior DVR also receives an ascending auditory input from the thalamus. The auditory target within the DVR of birds is termed field L [Karten, 1968; Bonke et al., 1979a, b; Kelley and Nottebohm, 1979; Brauth et al., 1987; Wild et al., 1993], but the auditory target in turtles, crocodilians and lizards has not been given a specific name [Pritz, 1974a; Ebner, 1976; Northcutt, 1978; Balaban and Ulinski, 1981; Bruce and Butler, 1984a, b; Belekhova et al., 1985; Brauth and Reiner, 1991]. This cell group has a similar location in birds and reptiles, however, as it is situated in the ventromedial part of the DVR somewhat caudal to the Vtt of the DVR. In birds, crocodilians and turtles, the neurons of this auditory field are multipolar in dendritic orientation and they receive direct input from a thalamic auditory nucleus that itself receives input from the central nucleus of the inferior colliculus [Karten, 1967; Pritz, 1974b; Northcutt, 1978; Belekhova et al., 1985]. In reptiles these thalamic and midbrain regions are termed nucleus reuniens and the torus semicircularis, respectively, whereas in birds they are termed nucleus ovoidalis and nucleus mesencephalicus lateralis pars dorsalis, respectively. Physiological studies have confirmed the auditory nature of field L in birds [Bonke et al., 1979a, b; Scheich et al., 1979], but the auditory physiology of the comparable region of the DVR in reptiles has not been extensively studied [Belekhova et al., 1985].

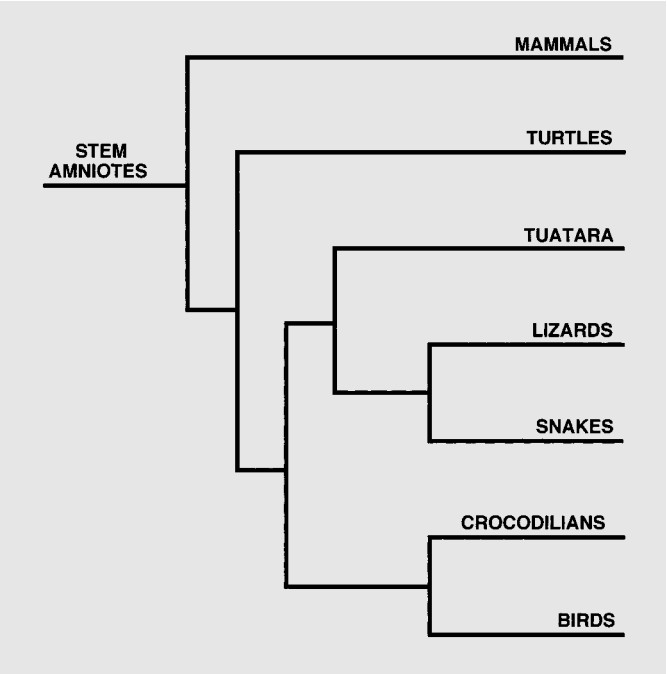


**Fig. 1.** Cladogram showing the phylogenetic relationships of the major reptilian groups to one another and to mammals and birds. Based on Gauthier et al. [1988].

Rhynchocephalians are lizard-like reptiles that are the sister group of squamates (lizards and snakes) (fig. 1) [Gauthier et al., 1988]. The tuatara *(Sphenodon punctatus)* is the only extant rhynchocephalian reptile and it appears to closely resemble fossil rhynchocephalians, implying retention of primitive rhynchocephalian traits. Unlike in birds, turtles, crocodilians, snakes and lizards, the DVR of *Sphenodon* is not organized into a continuous field of neighboring neuronal cell groups [Elliot-Smith, 1919; Hines, 1923; Durward, 1930; Northcutt, 1978]. Rather, the DVR of *Sphenodon* possesses a three-layered architecture, with the major neuron-rich layer being a neuronal cell plate that cytoarchitecturally resembles the cortical neuronal cell plate (fig. 2).

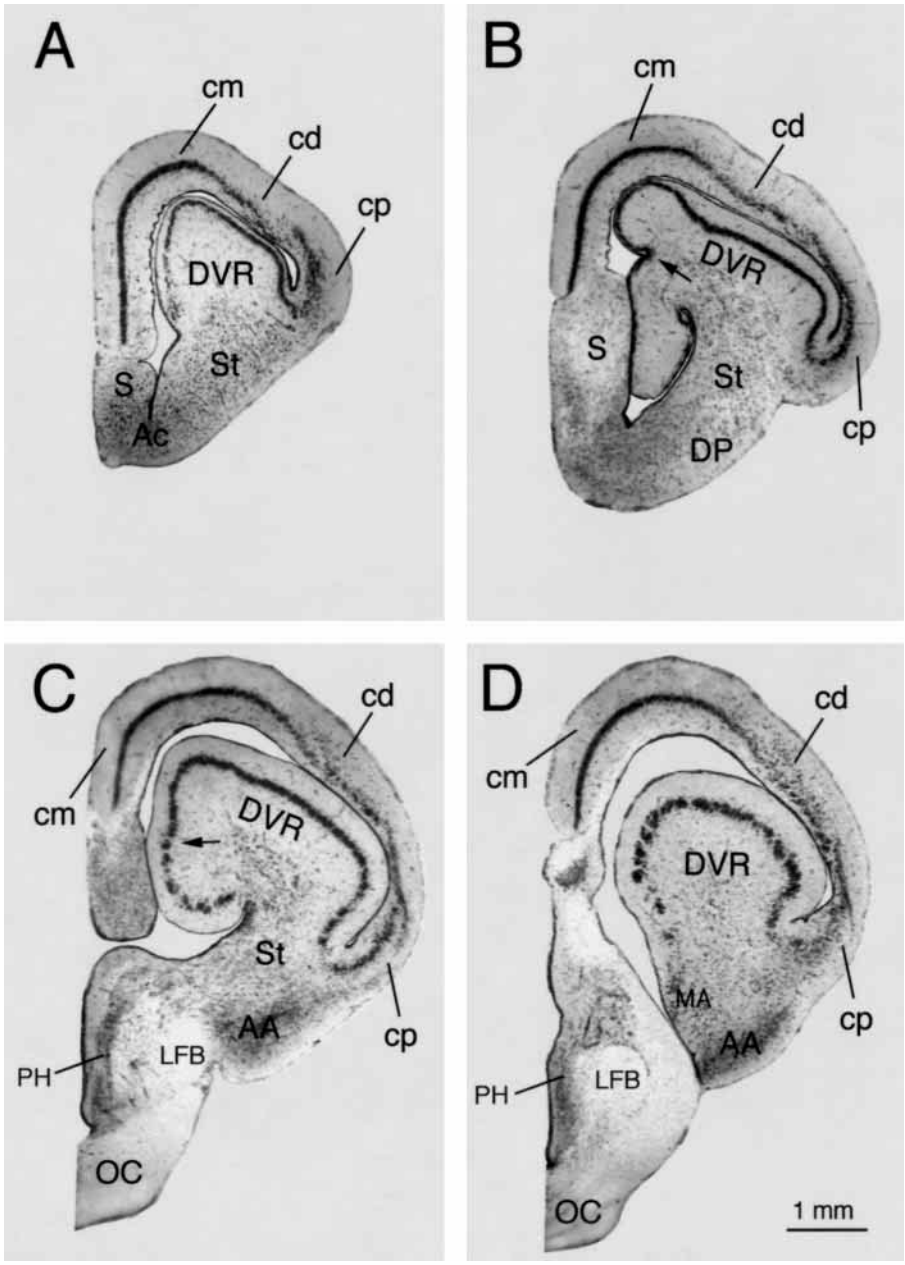


**Fig. 2.** Images of a rostral (**A**) to caudal (**D**) series of cresyl violet-stained transverse sections through the telencephalon of *Sphenodon punctatus*. Note that the DVR of *Sphenodon* possesses a three-layered cytoarchitecture that resembles that of the cortical cell plate. The arrow in **B** marks a sulcus in the ventral DVR below which the cell plate becomes juxtaposed to the ependyma, resulting in loss of a distinct ependymal layer. The arrow in **C** marks a site below which the caudal DVR cell plate becomes broken into cell clusters. At the caudal level shown in **D**, the entire DVR cell plate is broken into a series of clusters. Abbreviations: AA = Anterior amygdala; Ac = nucleus accumbens; cd = dorsal cortex; cm = medial cortex; cp = pyriform cortex; DP = dorsal pallidum; DVR = dorsal ventricular ridge; LFB = lateral forebrain bundle; MA = medial amygdala; OC = optic chiasm; PH = periventricular hypothalamus; S = septum; St = striatum.

The neurons of the DVR cell plate, which is continuous with the cell plate of the dorsal cortex/pallial thickening at very rostral telencephalic levels and with the cell plate of the lateral cortex at all other telencephalic levels, appear to extend their apical dendrites toward the center of the DVR [Northcutt, 1978]. The neurons of the DVR cell plate also possess basal dendrites that extend into a cell free zone that separates them from the ependyma of the DVR. Thus, except for its involution, the DVR of *Sphenodon* possesses a cytoarchitecture closely resembling the three-layered architecture characteristic of the telencephalic cortex of reptiles [Northcutt, 1978; Ulinski, 1988; Reiner, 1991, 1993].

The organization of the DVR in *Sphenodon* is of particular interest because its trilaminar structure might represent retention of the primitive condition for the DVR in reptiles. Analysis of DVR cytoarchitecture in extant nonrhynchocephalian reptiles supports this possibility [Northcutt, 1978]. For example, although no extant nonrhynchocepha-

lian reptile possesses a laminated DVR exactly resembling that of *Sphenodon*, turtles and the members of many different lizard families (such as gekkonids, anguids, scincids and lacertids) possess a DVR that in places has a periventricular cell plate consisting of closely spaced cell clusters [Riss et al., 1969; Northcutt, 1978]. It is of note that the caudal DVR of *Sphenodon* also has this periventricular cell cluster type cytoarchitectural appearance (fig. 2). In fact, at caudal DVR levels, the DVR of *Sphenodon* is indistinguishable from that of some lizard species [Northcutt, 1978]. By contrast, crocodilians, snakes and members of other lizard families (iguanids, agamids and chameleonids) do not possess such a periventricular cell plate and the DVR is entirely nuclear in cytoarchitecture [Northcutt, 1978]. From the viewpoint of cladistic analysis, the fact that turtles and disparate lizards possess a DVR with a partial cell plate suggests that these groups were derived from a common ancestor with a laminated DVR, presumably resembling that in *Sphenodon*, as it is unlikely that a DVR with periventricular cell clusters could have evolved independently in so many separate lineages from a nonlaminated DVR.

Regardless of its evolutionary relationship to a periventricular cell cluster-type DVR, it is of interest to establish whether the laminated DVR of *Sphenodon* receives visual and auditory imputs in its anterior part, similar to the nuclear DVR of birds and other reptiles. The demonstrated presence of a Vtt and A1 in the rostral DVR of such diverse sauropsids as turtles, lizards, crocodilians and birds supports the view that these DVR regions were likely present in the common reptile ancestor of living birds and reptiles (i.e. stem or basal reptiles). For this reason, the common ancestor of squamates and *Sphenodon* is likely to have possessed a Vtt and A1 in its anterior DVR. Nonetheless, it is of interest to determine if the laminated DVR of *Sphenodon* receives visual and auditory inputs in its anterior part, as does the nuclear DVR of birds and other reptiles, and where such inputs might terminate. A nucleus rotundus and a nucleus reuniens closely resembling those of turtles in cytoarchitecture are present in *Sphenodon* [Hines, 1923; Durward, 1930], which suggests that these nuclei are likely to at least project to the telencephalon. Although the scarcity and protected status of *Sphenodon* precludes obtaining sufficient animals to carry out conventional anterograde pathway tracing studies, there is an alternative approach that can serve this purpose and does not require sacrificing numerous specimens of *Sphenodon*. Many studies in birds and nonrhynchocephalian reptiles have shown that the neuropil of the visual and auditory areas within the DVR are rich in the glycolytic enzyme succinic dehydrogenase (SDH). The abundance of this enzyme in these regions appears to reflect the presence of highly metabolically active terminals from nucleus rotundus and the auditory thalamus [Masai et al., 1966; Baker-Cohen, 1968; Pritz and Northcutt, 1977; Northcutt, 1978]. We therefore carried out a study on a specimen of *Sphenodon* in which we used SDH histochemistry to determine if visual and auditory fields might also be present in its DVR. In addition, we used acetylcholinesterase (AChE) histochemistry to determine the extent of the DVR relative to the basal ganglia.

## Material and Methods

The single specimen of *Sphenodon punctatus* used in this study was obtained from New Zealand with the permission of the Secretary of the Interior. The *Sphenodon* was anesthetized with Nembutal and decapitated. The brain was then rapidly removed and placed in a plastic embedding mold containing a commercially prepared, water soluble resin. The brain, resin and mold were all immersed in 2-methyl-butane cooled to –7 °C with dry ice and were thereby frozen. The entire brain was then cut into twenty-five micron sections in the transverse plane at –20 °C on a Harris cryostat. The sections were collected on gelatin coated slides and dried for 10 min in a vacuum desiccator at room temperature. The slide-mounted sections were stored at –20 °C until processed for histochemistry.

Alternate series of sections were reacted by AChE and SDH histochemistry. For AChE histochemistry [Gomori, 1952; Northcutt, 1974; Pritz and Northcutt, 1977], sections were incubated for 10–60 min at 37 °C in 200 mg acetylthiocholine iodide in 100 ml of a stock solution containing 150 mg copper sulfate, 190 mg glycine, 500 mg magnesium chloride, and 900 mg maleic acid in 15 ml 4% sodium hydroxide and 85 ml 40% $Na_2SO_4$, with the final solution adjusted to pH 6.0. The slide-mounted sections were then rinsed three times in saturated $Na_2SO_4$ and immersed in ammonium sulfide for 2 min. A standard histochemical procedure was used to localize SDH activity in the slide-mounted sections of *Sphenodon* brain [Pearse, 1960; Northcutt, 1974]. In brief, the sections were incubated for 30 min at 37 °C in an incubation medium containing 17.7 g sodium succinate and 100 mg nitro blue tetrazolium (NBT) in 250 ml 0.05 *M* sodium phosphate buffered saline, with the final solution adjusted to pH 7.2–7.4. Progress of the reaction for both AChE and SDH was assessed by visual examination of the tissue. All sections were then stained with cresyl violet, dehydrated, cleared and coverslipped with Permount. The tissue was then examined with an Olympus BHS transmitted light microscope. Images of AChE and SDH labeling presented in this paper were prepared digitally using the illustrating program Adobe Photoshop v4.0, and histological imperfections were removed using this program.

## Results

Due to the atypical morphology of the DVR in *Sphenodon*, we will first describe its cytoarchitecture. In the subsequent two parts of the Results section, we will present the AChE data and then the SDH data.

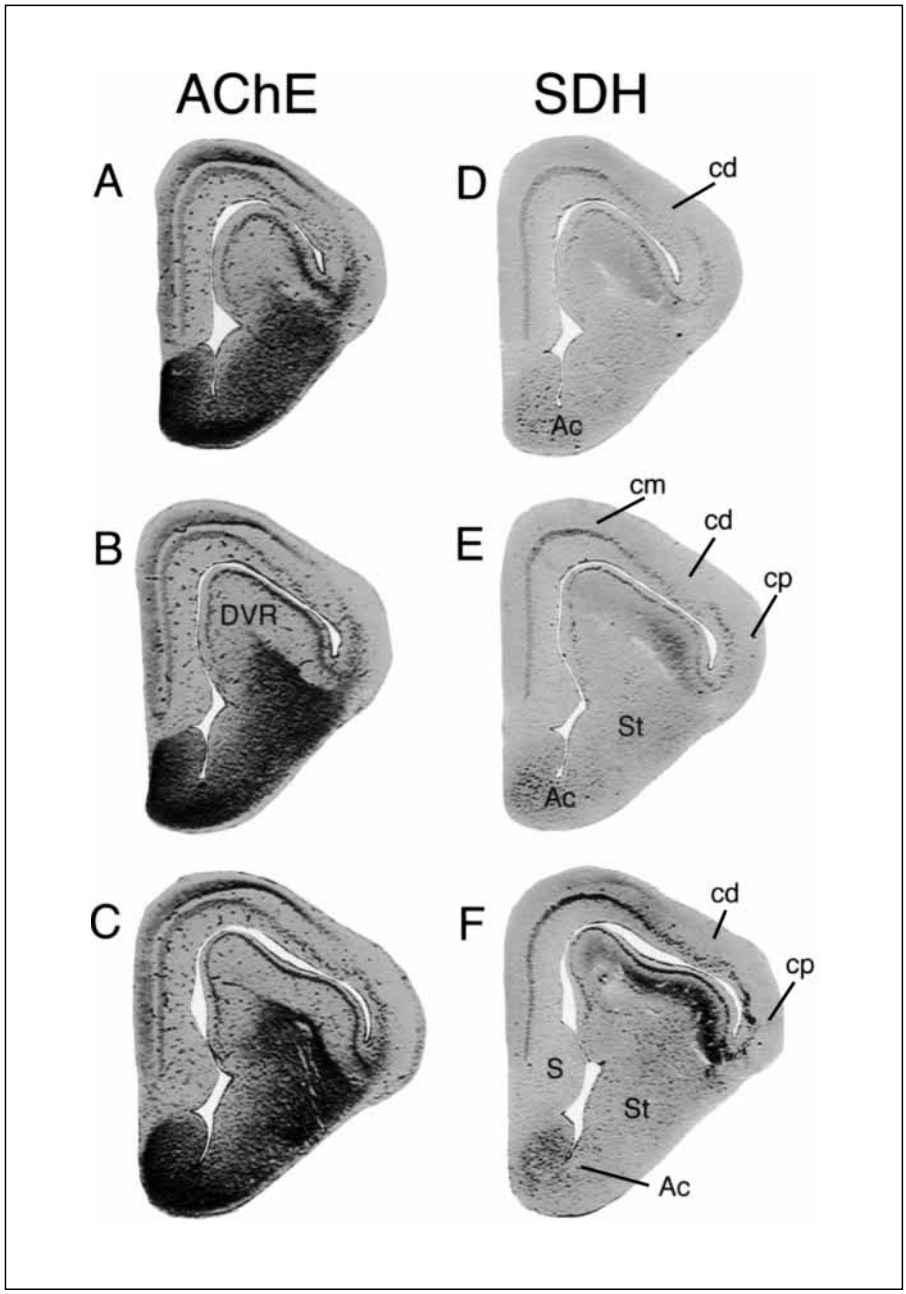


**Fig. 3.** Images of acetylcholinesterase (AChE; **A**–**C**) and succinic dehydrogenase (SDH; **D**–**F**) labeling in a rostral (**A** and **D**) to caudal (**C** and **F**) series of matched transverse sections through the rostral telencephalon of *Sphenodon punctatus.* AChE and SDH labeling appears as optically dense areas in the images. The cell plates of the cortex and the DVR are optically dense because the tissue had been counterstained with cresyl violet. Abbreviations: Ac = Nucleus accumbens; cd = dorsal cortex; cm = medial cortex; cp = pyriform cortex; DVR = dorsal ventricular ridge; S = septum; St = striatum.

*DVR Cytoarchitecture.* The anterior DVR of *Sphenodon* possesses a continuous cell plate that cytoarchitecturally resembles the cortical cell plate (fig. 2). The neurons of this DVR cell plate are continuous with the cell plate of the dorsal cortex/pallial thickening at the rostralmost telencephalic levels and with the cell plate of the lateral cortex at all other telencephalic levels. The DVR cell plate neurons have been reported to extend their apical dendrites toward the center of the DVR [Northcutt, 1978]. This apical zone appears comparable to the molecular layer of the telencephalic cortex, and appears to be continuous with it. As true of the cortical molecular layer in *Sphenodon,* the DVR molecular layer of *Sphenodon* contains scattered neurons that appear to possess a non-pyramidal morphology. The neurons of the DVR cell plate extend basal dendrites into a cell free zone that separates them from the ependyma of the DVR. This zone is continuous with the ependymal layer of the telencephalic cortex, and like the molecular layer of DVR it contains a

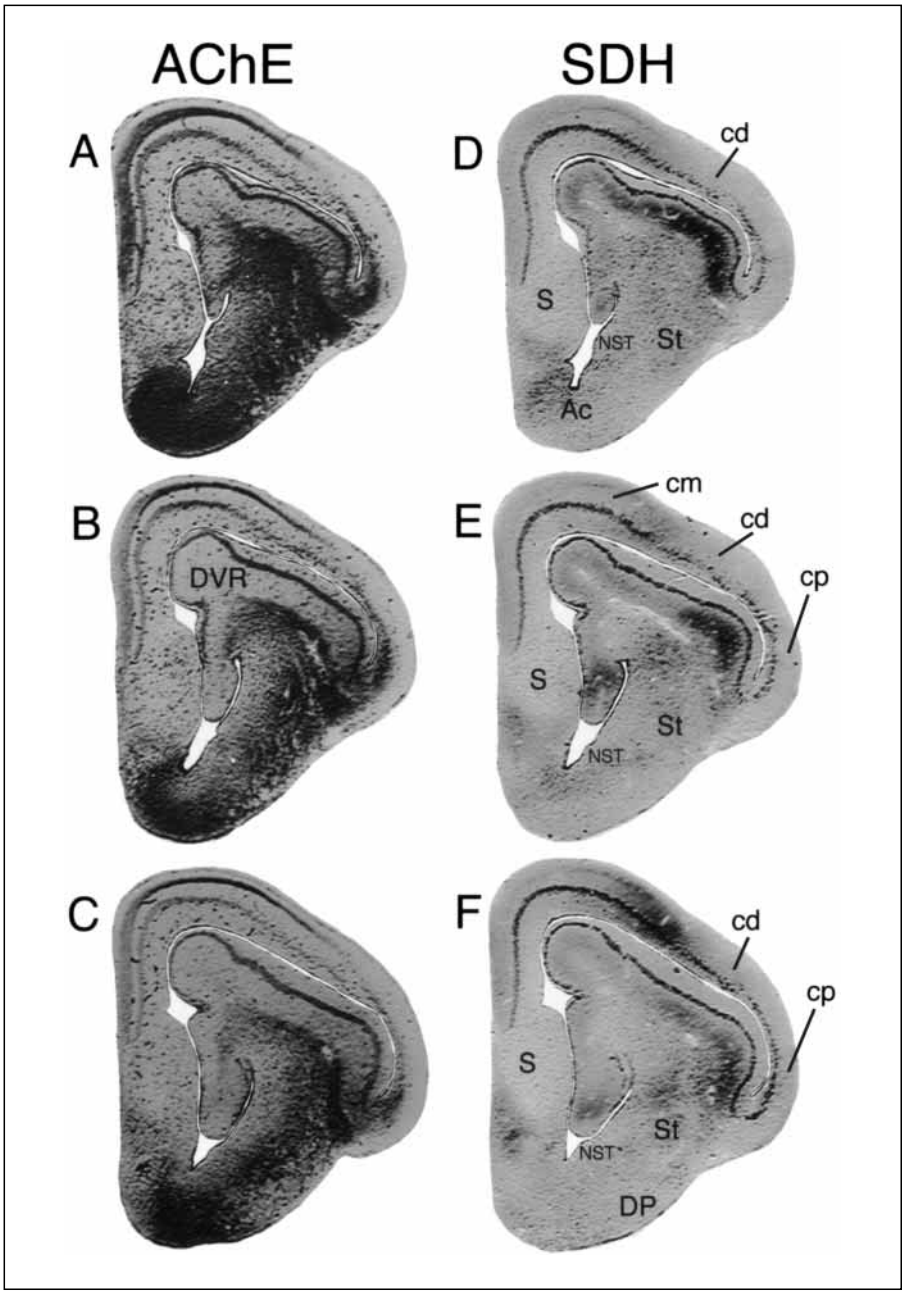


**Fig. 4.** Images of acetylcholinesterase (AChE; **A**–**C**) and succinic dehydrogenase (SDH; **D**–**F**) labeling in a rostral (**A** and **D**) to caudal (**C** and **F**) series of matched transverse sections through the telencephalon of *Sphenodon punctatus* at slightly more caudal levels than shown in figure 3. AChE and SDH labeling appears as optically dense areas in the images. The cell plates of the cortex and the DVR are optically dense because the tissue had been counterstained with cresyl violet. Abbreviations: Ac = nucleus accumbens; cd = dorsal cortex; cm = medial cortex; cp = pyriform cortex; DP = dorsal pallidum; DVR = dorsal ventricular ridge; NST = nucleus of the stria terminalis; S = septum; St = striatum.

few scatterred neurons with a non-pyramidal morphology, as is also true of the epi-ependymal layer of the cortex in *Sphenodon.* Thus, the DVR of *Sphenodon* possesses a cytoarchitecture closely resembling the three-layered architecture characteristic of its telencephalic cortex. The cell plate of the DVR is not uniform in its cytoarchitecture throughout the rostro-caudal extent of the DVR. The ependymal layer of the ventral tip of parts of the rostral DVR is absent, and at these levels the cell plate abuts the ependyma (fig. 2B). At caudal levels of the DVR, all of the cell plate or only its ventral part is broken into a continuous series of neuronal cell clusters (fig. 2C, D).

*AChE.* The ventrolateral and ventromedial telencephalic walls at and anterior to the anterior commissure were very rich in AChE labeling (fig. 3–5). The region of intense staining in the ventrolateral wall was within the region previously identified as the striatum in *Sphenodon* [Northcutt, 1978]. This region extended as far dorsally as the level at

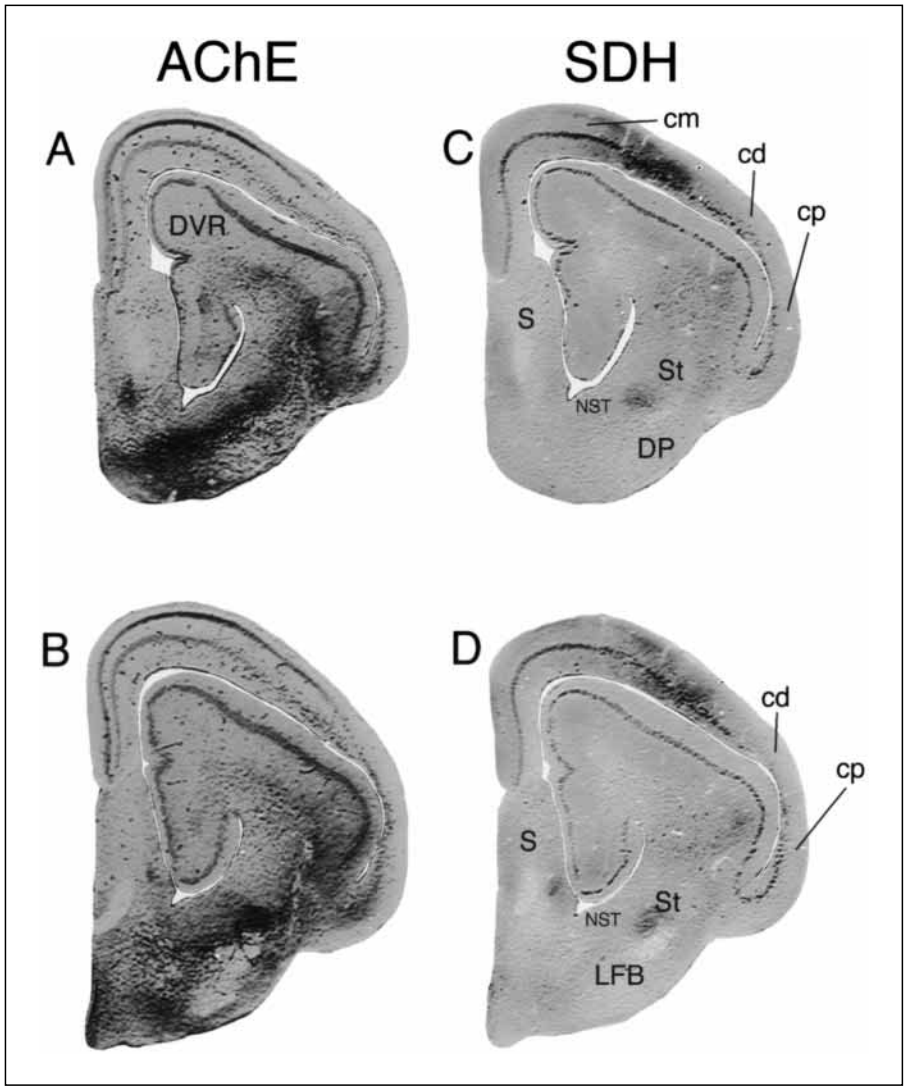


**Fig. 5.** Images of acetylcholinesterase (AChE; **A**–**B**) and succinic dehydrogenase (SDH; **C**–**D**) labeling in a rostral (**A** and **C**) to caudal (**B** and **D**) series of matched transverse sections through the telencephalon of *Sphenodon punctatus* at slightly more caudal levels than shown in figure 4. AChE and SDH labeling appears as optically dense areas in the images. The cell plates of the cortex and the DVR are optically dense because the tissue had been counterstained with cresyl violet. Abbreviations: cd = dorsal cortex; cm = medial cortex; cp = pyriform cortex; DP = dorsal pallidum; DVR = dorsal ventricular ridge; LFB = lateral forebrain bundle; NST = nucleus of the stria terminalis; S = septum; St = striatum.

which the middle cerebral artery courses through the ventral part of the DVR [Elliot-Smith, 1919] and thus defined the border between the DVR and the striatum. Regions of poor AChE labeling in the ventrolateral and ventromedial aspects of the AChE-rich field of the ventrolateral telencephalic wall appear to correspond to the dorsal pallidum (which also can be called the globus pallidus) and the nucleus of the stria terminalis, respectively, as identified in turtles and pigeons [Reiner, 1987; Reiner et al., 1984, 1998; Fowler et al., 1999]. The AChE-rich field in the rostral ventromedial telencephalon that surrounds the inferior aspect of the lateral ventricle appears to correspond to the nucleus accumbens septi [Parent and Olivier, 1970]. AChE staining in the septal region above the AChE-rich region of the ventromedial wall tended to be poor. The DVR was poor in AChE staining (fig. 3–5). A thin band of intense AChE labeling was present in the pallium, parallel and just deep to the pial surface. This thin band was located in the upper part of the molecular layer and it extended from the medial edge of the dorsal cortex, over the lateral edge of the medial cortex (where it abuts the dorsal cortex), to the ventral tip of the medial cortex (fig. 3–5).

*SDH.* We found a region conspicuously rich in SDH in the neuropil below the cell plate of the rostrolateral DVR (fig. 3–5). This SDH-rich zone was located within the region of the apical dendrites of the neurons of the overlying cell plate, and it extended from rostral to mid-DVR levels. At its widest point, the SDH-rich region extended from the lateral to the medial edge of the dorsal part of the DVR cell plate, thereby occupying the full mediolateral expanse of the

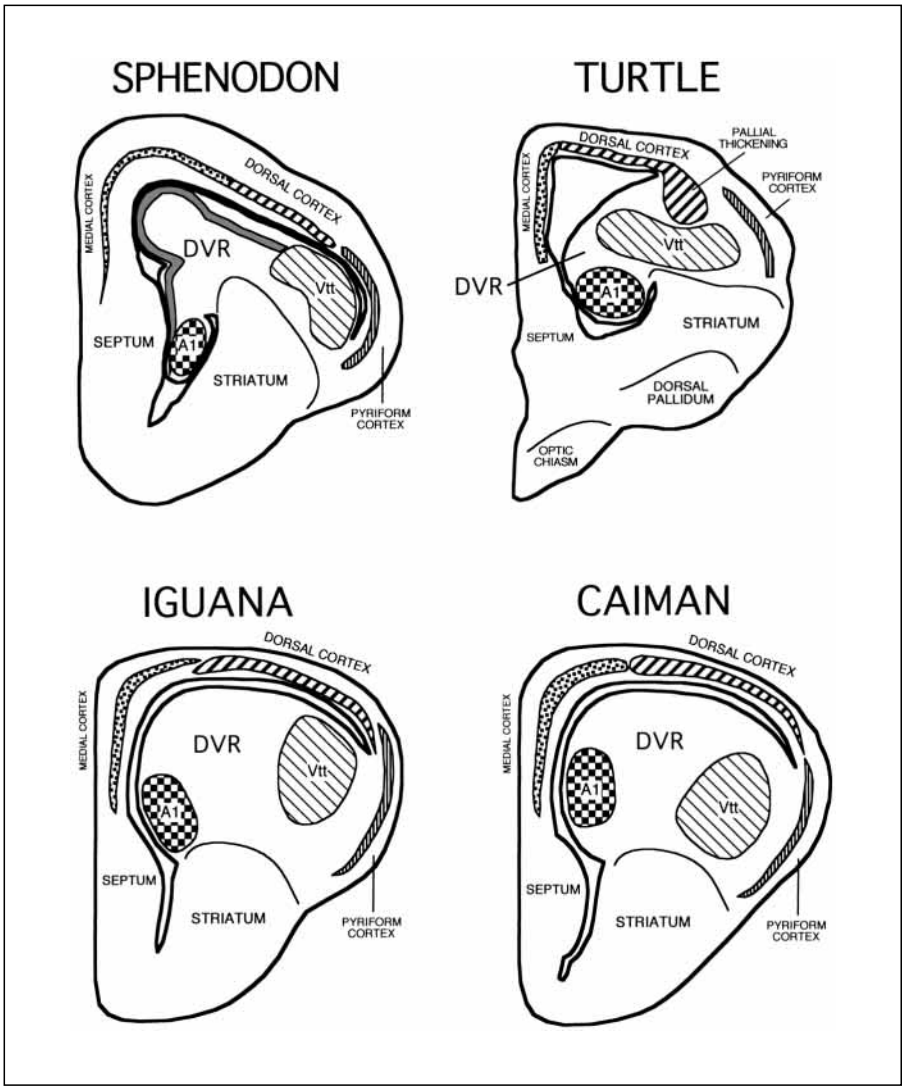


**Fig. 6.** Schematic drawings of transverse sections comparing the location of visual (Vtt) and auditory (A1) zones within the DVR of a turtle, an iguana and a caiman as revealed by succinic dehydrogenase (SDH) histochemistry to those in *Sphenodon* suggested by our present data. The location of the visual and auditory areas have been confirmed for turtle, iguana and caiman by pathway tracing studies. The location of Vtt and A1 depicted for *Sphenodon* include the part of the adjacent DVR cell plate, because it seems likely that the neurons of these regions receive the sensory thalamic input. Note that the locations of the visual (Vtt) and auditory (A1) zones are very similar among the reptilian groups shown. Abbreviations: Vtt = tectothalamorecipient visual zone of the DVR; A1 = thalamorecipient auditory zone of the DVR.

dorsal part of the DVR. At least the lateral part of this field resembles by position the telencephalic target (Vtt) of the visual tectothalamofugal pathway described in birds and other reptiles (fig. 6). An oval, slightly less SDH-rich neuropil was observed deep to the cell plate of the ventromedial DVR (fig. 4E). This SDH-rich region did not extend as far rostrally as the SDH-rich region of the dorsal DVR, and the cell plate external to it was not as distinct as that of the dorsal DVR. This field resembles by position the primary auditory area (A1) of the DVR described in birds and other reptiles, which receives input from the auditory thalamus (fig. 6). The remainder of DVR and cortex was poor in SDH labeling, although at levels just caudal to the SDH-rich region of the laterodorsal DVR some labeling was observed throughout the full depth of the lateral part of the medial cortex and the medial part of the dorsal cortex where they abut one another (fig. 3–5). The ventrolateral and ventromedial telencephalic walls were generally poor in SDH staining, although punctate (presumably cellular) labeling was evident in the medial part of nucleus accumbens septi.

## Discussion

The present study provides what we believe is strong evidence for the existence and location of the thalamorecipient visual and auditory fields in the anterior DVR of *Sphenodon punctatus.* Hodological studies show that the SDH-rich fields in the dorsolateral and ventromedial DVR of birds, crocodilians and turtles correspond to the thalamorecipient

visual and auditory portions of the anterior DVR [Masai et al., 1966; Baker-Cohen, 1968; Pritz and Northcutt, 1977; Northcutt, 1978; Pritz, 1980; Karten, 1991]. The SDH-rich visual part of the anterior DVR receives input from nucleus rotundus, whereas the SDH-rich auditory part of the anterior DVR receives input from a thalamic region called nucleus reuniens in reptiles and nucleus ovoidalis in birds. A nucleus rotundus and a nucleus reuniens that bear close cytoarchitectural resemblance to those found in turtles are present in *Sphenodon punctatus* [Durward, 1930]. These observations support the interpretation that the SDH-rich zone in the rostrolateral anterior DVR of *Sphenodon* represents the zone of termination of nucleus rotundus input, whereas the SDH-rich zone in the ventromedial anterior DVR of *Sphenodon* represents the zone of termination of nucleus reuniens input (fig. 6). These conclusions further support the view that the presence of a Vtt and an A1 in the anterior DVR is primitive for sauropsids and that both were thus present in an anterior DVR in basal reptiles [Northcutt, 1981]. Our conclusions also have implications for the cytoarchitecture of this ancestral DVR and the organization of its thalamic inputs, as detailed below.

In neither the case of the putative visual nor the putative auditory input to the DVR of *Sphenodon* does this input appear to end on the perikarya of the DVR target neurons, as the presumed terminal fields are found at the distal apical dendritic arbors of these neurons. Additionally, the presumed terminal fields of visual and auditory input in the anterior DVR of *Sphenodon* contain only scattered perikarya, the majority of which contain neuropeptide Y or LANT6 [unpubl. observ.], which have been shown to be interneuron markers in other reptilian and avian species [Reiner and Carraway, 1987; Reiner and Oliver, 1987; Anderson and Reiner, 1990; Reiner, 1993; Reiner and Anderson, 1993]. In this regard, the presumed thalamic input to the DVR of *Sphenodon* resembles that of the dorsal lateral geniculate nucleus to the dorsal cortex and pallial thickening in turtles, which also ends primarily on the distal apical dendrites of the neurons of the cortical cell plate, as well as on some local circuit neurons within the terminal field itself [Ulinski, 1988; Reiner, 1993]. In the case of the dorsal cortex and pallial thickening, however, the input ends along the pial surface. By contrast, because of the periventricular orientation of the cell plate of its DVR, the presumed visual and auditory thalamic input appears to end deep to the DVR cell plate in *Sphenodon.* This zone of termination appears to be topologically continuous with and comparable to the molecular layer of cortex. Whether any medial part of the SDH-rich zone of the dorsal DVR in *Sphenodon* corresponds to the SDH-rich somatosensory-recipient medial part of the DVR that has been demonstrated in turtles, lizards and crocodilians is uncertain [Baker-Cohen, 1968; Pritz and Northcutt, 1977; Northcutt, 1978; Balaban and Ulinski, 1981]. Note that a dorsal lateral geniculate nucleus resembling that in turtles is present in *Sphenodon* [Durward, 1930]. This raises the possibility that a primary visual area is present in dorsal cortex/pallial thickening in *Sphenodon* (presumably rostrally) and receives input from the dorsal lateral geniculate nucleus at its pial surface. Under these circumstances, both the cell plates of the dorsal cortex/pallial thickening and DVR and the target zones of sensory thalamic input adjacent to them would likely be, at least in part, topologically continuous in *Sphenodon.*

It is not known whether the cytoarchitecture of the DVR found in *Sphenodon* represents retention of the primitive condition for the DVR in reptiles and birds (i.e. the one present in the reptile group that was the common ancestor of all sauropsids). This issue is important for understanding the evolution of the DVR. If, in fact, the DVR condition in Sphenodon has been retained from the condition found in stem reptiles, there are two major implications. First, it would imply that the DVR arose as a cell plate that was much like the dorsal cortex of turtles and *Sphenodon* in its cytoarchitecture. Secondly, retention of the primitive DVR condition in the lineage leading up to the divergence of rhynchocephalians and squamates would imply that it must also have been the condition at the divergence between archosaurs and the lineage leading to rhynchocephalians and squamates, as well as at the divergence of turtles from the lineage leading to diapsid reptiles (fig. 1). This would unavoidably imply that the differentiation of DVR into cell groups occurred separately in each major reptilian lineage (i.e. turtles, archosaurs and squamates). This would then explain the slight differences among these reptilian groups in the location and shape of the rotundorecipient and reuniens-recipient parts of the DVR [Johnston, 1915; Northcutt, 1978; Pritz, 1980]. It is possible that the break-up of the DVR cell plate into distinct cell clusters in parts of the *Sphenodon* DVR and in much of the DVR of turtles and some lizard species represents a stage in this differentiation and migration of the cell plate neurons out of the cell plate.

Several considerations suggest that a trilaminar DVR, such as in *Sphenodon,* is likely to be the primitive condition. First, among turtles, which are thought to be the first extant reptilian group to diverge from the stem reptile lineage [Reisz and Laurin, 1991; Lee, 1997], the DVR is somewhat laminated, as its medial and ventral ependymal edge is lined with cell clusters [Johnston, 1915; Balaban and Ulinski, 1981]. This lamination is especially evident in the most primitive extant group of turtles, the pleurodires (side-

necked turtles) [Riss et al., 1969]. Secondly, the distribution of a semi-laminated DVR (i.e. with periventricular cell clusters and a central cell mass) among lizard species suggests that a laminated DVR is the primitive condition among lizards [Northcutt, 1978]. Thus, our findings that the DVR in *Sphenodon* appears to receive visual and auditory input, as in other reptiles, suggests that the thalamic sensory input to DVR in the common ancestor of living reptiles (i.e. stem reptiles for the reptilian clade) might have been organized (i.e. axodendritic) much like the thalamic sensory input to dorsal cortex in living reptiles, and the DVR could have had a cytoarchitecture much like that of dorsal cortex in the stem reptiles from which all living reptiles evolved. Neither the present data nor a cladistic analysis can resolve whether the stem amniotes from which stem reptiles and mammals both evolved possessed a DVR, some rudimentary proto-DVR or no DVR whatsoever [Hopson, 1979; Reiner, 1993; Butler, 1994a, b; Northcutt and Kaas, 1995]. If the stem amniotes did possess a DVR or proto-DVR, the present considerations suggest that this structure would be likely to have possessed a trilaminar cytoarchitecture resembling that of reptilian dorsal cortex and like dorsal cortex it would probably have received thalamic sensory input at the apical dendrites of the neurons of its cell plate. In the case of the dorsal cortex, this input would have arisen from the portion of the thalamus that Butler [1994a, b] has termed the lemnothalamus, whereas for the DVR the input would have arisen from the so-called collothalamus.

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