Chapter 4

Evolution of Thalamic Sensory Centers in Amniotes: Phylogeny and Functional Adaptation

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Abstract

This chapter is a continuation of our previous study of the forebrain evolution in vertebrates using some new tests allowing evolutionary transformations to be revealed. As such tests, we chose the expression of calcium-binding proteins as neuronal functional markers and the metabolic activity of cytochrome oxidase, characterizing the level of neuronal activity. Here, we report the results of our study of the thalamic visual and auditory centers in reptiles (turtles, *Emys orbicularis* and *Testudo horsfieldii*) and birds (pigeon, *Columba livia*) with a special focus on differences in their parallel visual thalamofugal and tectofugal channels and auditory lemniscal and extralemniscal channels. A comparison with data obtained in other Sauropsida amniotes was drawn to elucidate the role of phylogenetic and functionally adaptive factors determining variable distribution of calcium-binding proteins and metabolic activity, as well as to identify evolutionary conservative and plastic traits in the organization of these thalamic sensory centers.

Keywords: visual system, auditory system, Ca-binding proteins, metabolic activity, Sauropsida amniotes, evolution

1. Introduction

Since the creation of Charles Darwin's theory of evolution [1], most studies in the field of evolutionary neuroscience were focused mainly on the phylogenetic continuity in the evolution of the central nervous system in vertebrates. A central problem of comparative neurobiology was a search for homologous brain structures in different taxa of vertebrates through the identification of common ancestral (plesiomorphic) and acquired (apomorphic) traits (see for references [2–4]). At the same time remarkable diversity of brain structures in every vertebrate divergent lineage is a result of two evolutionary pathways – phylogenetic history and adaptive

specialization (apomorphosis and idioadaptation according to Severtsov [5]). The second pathway is a key in the origin of homoplasy (parallel and convergent evolution). Two non-antagonistic but rather complementary approaches – historical (phylogeny) and causal (evolving adaptive mechanisms) Dobzhansky considered necessary for the evolutionary synthesis [6]. A combination the embryogenetic, morphological, histochemical and functional approaches as well as the introduction of modern molecular and genetic methods led to a partial or even total revision of some classical views of brain evolution. One of the most crucial achievements was the revision of the old concept of the homology between the basal ganglia and isocortex in Sauropsida amniotes and mammals. According to the new concept, a great part of the avian and reptilian telencephalon, previously considered as a homolog of the striatum, has a pallial origin and is homologous to the mammalian cortex. Like in mammals, the basal ganglia (striatopallidum) occupy only the ventral part of the telencephalic hemisphere. On this basis, the nomenclature of telencephalic structures in birds has been modified [7–10]. Birds were thus rehabilitated as possessors of the highly developed pallium as compared to the telencephalic cortex in mammals. Behavioral studies conducted in various species of birds and reptiles also led to the reevaluation of their cognitive capabilities, in some avian species as compared to those in primates [9, 11–13]. However, the issues of what parts of the mammalian cortex are homologous to the avian telencephalic pallial parts targeted by the thalamic relay nuclei still remain a matter of indefatigable debate.

While the homology of the thalamofugal (geniculocortical) pathway in amniotes is now generally accepted, two alternative hypotheses have been advanced regarding the homology of the thalamopallial tectofugal and auditory pathways. According to the "neocortex hypothesis, " the thalamic projection fields in the pallium of birds and reptiles are homologous to the mammalian isocortex (a dorsal pallium derivative) [7, 8, 10, 14, 15]. The "claustroamygdalar hypothesis" draws a homology between them and a part of the claustroamygdalar complex (a ventral/lateral pallium derivative) [4, 16, 17]. Respectively, thalamic projection nuclei in reptiles and birds are comparable either with dorsothalamic relay nuclei in mammals ("neocortex hypothesis") [8, 10, 14, 15] or a part of the thalamic complex of intralaminar and posterior nuclei ("claustroamygdalar hypothesis") [4, 16, 18]. There is no final solution for this problem.

2. Results and their evolutionary implications

Phylogenetic transformations in the sensory thalamo-telencephalic systems were considered by the classics of comparative neurology as critical for understanding the forebrain evolution. In the laboratory of A.I. Karamian, the visual, auditory and somatosensory systems were investigated for many years (1958–1989) in the wide range representatives of different vertebrate classes. It was established that these systems consist of parallel pathways, having different morphological and functional characteristics, and different rates of phylogenetic development (see Refs. [19–22]).

We are carrying out comparative studies of the visual and auditory systems in amniotes, and birds (Archosauria), descending from a common ancestor and thus, having a key significance for understanding the forebrain evolution. As new complementary tests, characterizing the

organization of the visual and auditory centers, we used: (1) immunohistochemical analysis of expression of parvalbumin (PV) and calbindin (CB), calcium-binding proteins serving as functionally selective neuronal markers and (2) histochemical evaluation of cytochrome oxidase (CO) metabolic activity reflecting the level of neuronal functional activity. Expression of calcium-binding proteins was studied using the standard procedure of immunohistochemistry on free-floating 40 μm sections. Monoclonal mouse anti-PV (Sigma, USA) diluted 1:1000 and polyclonal rabbit anti-CB (Swant, Switzerland) diluted 1:5000 were used. Cytochrome oxidase activity was revealed on free-floating 40 μm sections according to the convenient histochemical method using cytochrome c from bovine heart, type III (Sigma, USA) as well. Sections were observed and analyzed using the microscope Zeiss Axio Imager A1 (Zeiss, Germany). Images were taken from representative sections with the digital camera mounted on the microscope. Digital images were created using Adobe Photoshop 7.0 (Adobe Systems Incorporated, USA) and assembled into montages. General adjustments of color, contrast, and brightness were made.

This chapter offers a brief comparative survey of our previously published and recently obtained results in the thalamic visual and auditory centers in turtles and pigeons, as well as their analysis in the light of the relevant literature data and present knowledge in this field. We set ourselves the task of elucidating: (1) to what extent the patterns of PV and CB immunoreactivity coincide in homologous centers of reptiles and birds; (2) whether the expression of PV and CB correlates with CO activity; and (3) whether these data can shed light on the role of the phylogenetic and functional (adaptive) factors in determining the PV and CB specificity of the sensory centers.

2.1. Visual system

Across all sauropsids (nonarchosaurian reptiles, Archosauria: birds and crocodiles), the visual system includes two main pathways projecting to the telencephalon, tecto- and thalamofugal, that have different properties. Within the tectofugal pathway in reptiles and birds, projections of retinal ganglion cells successively relay in the optic tectum, thalamic nucleus rotundus (Rot), which further projects to the visual dorsolateral region of the anterior dorsal ventricular ridge (ADVRdl) in reptiles and to the entopallium (Ent) in birds. Within the thalamofugal pathway, retinal ganglion cells directly project to the thalamic relay nucleus geniculatus lateralis, pars dorsalis (GLd), which then projects, in reptiles, to the dorsolateral cortex and, in birds, to the hyperpallial Wulst. Homology between these systems in reptiles and birds is generally accepted. They are comparable, according to "neocortex hypothesis, " to the mammalian thalamo (nucleus lateralis posterior+pulvinar)-extrastriate and geniculo-striate systems, respectively [3, 8–10].

Our results show that the tectofugal thalamic center Rot has a higher metabolic (CO) activity both in turtles (**Figure 1a-c**) and pigeons (**Figure 1d**, **f**) as compared to the thalamofugal center GLd. This correlates with the leading role of the tectofugal (collothalamic and extralemniscal) visual system in visual behavior [3]. Differences in the level of CO activity between the Rot and GLd are less significant in pigeons, probably due to a more highly developed thalamofugal visual system in birds.

As for the CaBPr immunoreactivity, the Rot in reptiles and birds differs by the distribution, ratio of PV- and CB-ir neurons, and intensity of their labeling. In the turtle Rot, strongly labeled

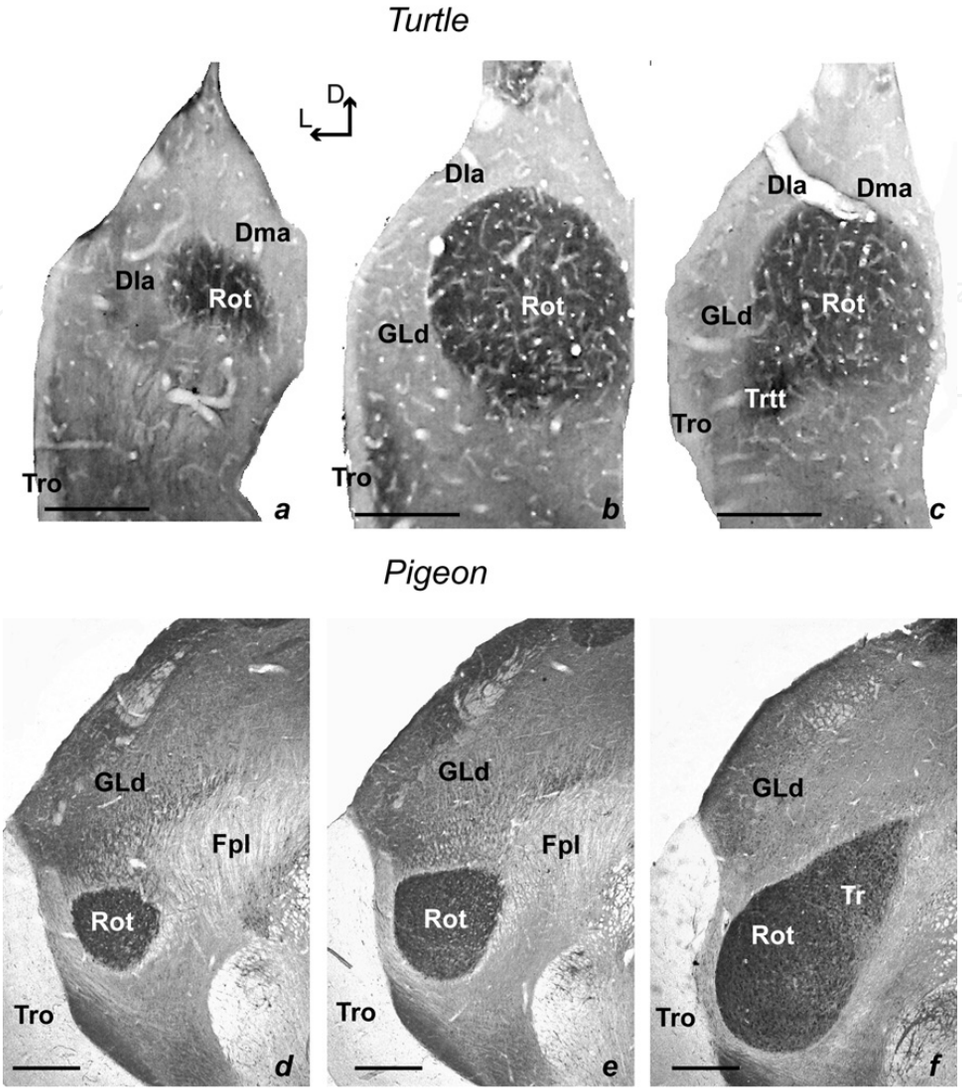

Figure 1. The activity of cytochrome oxidase in visual centers of turtles and pigeons. Rostrocaudal transverse unilateral sections of the thalamus in turtle (a-c) and pigeon (d-f). Note a high CO activity in the rot and a weaker CO activity in the GLd, both in turtle and pigeon. CO—Cytochrome oxidase; Dla—N. Dorsolateralis anterior; Dma—N. Dorsomedialis anterior; Fpl fasciculus prosencephali lateralis; GLd—*N. geniculatus* Lateralis, pars dorsalis; rot—*N. rotundus*; Tr—*N. triangularis*; Tro—Tractus opticus; Trtt—Tractus tectothalamicus. D—Dorsal; and L—lateral sides. Dorsal and lateral sides are the same here and in other figures. Scale bar: 500 μm.

CB-ir cells prevailed (**Figures 2b** and **3a**), whereas PV-ir cells were less numerous (**Figures 2b** and **3b**). On the contrary, in the pigeon Rot, strongly labeled PV-ir neurons were prevailing, whereas CB-ir cells exhibited a restricted distribution pattern and mainly weak labeling (**Figures 2d** and **3c**). In the triangular part of the Rot (Tr), strongly labeled PV- and CB-ir cells were observed to overlap (**Figures 2d** and **3c**, **d**). According to multiple studies in other reptilian and avian species, a great interspecies variability was found in the number of PV- and CB-ir neurons, ranging from the mixed content of both types to the existence of only one of them (see for Refs. [23, 24]). At the same time, both in turtles and pigeons, the Rot has an abundant PV innervation (**Figure 3d** along with a high CO activity (**Figure 1a**–**f**). In birds, the tectorotundal pathway contains multiple parallel channels, deriving from different types of

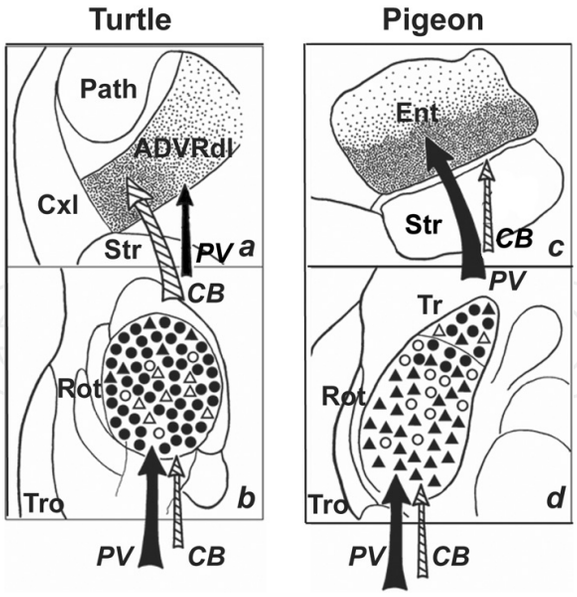

Figure 2. Different specificity to parvalbumin and calbindin of rotundo-telencephalic pathways in turtle (a, b) and pigeon (c, d). Schematic drawings of unilateral transverse sections of the brain at the level of the rot (b, d) and telencephalic areas (a, c), receiving projections from the rot. Circles indicate CB-ir neurons, triangles indicate PV-ir neurons (black are for strongly, white are for weakly labeled cells), and dots indicate immunoreactive terminals. Black arrows mark PV-ir input and striped arrows mark CB-ir input. ADVRdl—Dorsolateral anterior dorsal ventricular ridge; CB—Calbindin; cxl—Cortex lateralis; Ent—Entopallium; path—Pallial thickening; PV—Parvalbumin; rot—*N. rotundus*; Str—Striatum; Tr—*N. triangularis*; And Tro—Tractus opticus.

tectal neurons [25, 26] and processing different aspects of visual information [27, 28]. We found that tectorotundal projection neurons in birds and reptiles expressed PV and CB [29, 30]. Thus, a heterogeneous distribution of PV and CB immunoreactivity in the avian and reptilian Rot may relate to different chemospecificity of parallel tectorotundal channels.

Both in the turtle GLd (**Figure 3a, b** and the largest GLd subnuclei (DLAmc, DLL) of pigeons (**Figure 3e, f**), strongly labeled CB-ir neurons prevailed with PV-ir cells being less numerous. The other avian GLd subnuclei were found to contain cells immunoreactive either to both proteins or only to PV, as in the LdOPT [24]. At the same time, both in turtles and pigeons, CO activity in the GLd was lower than in the Rot with an exception for the LdOPT, where it was very high. Similar to the Rot, there is a great interspecies variability in the patterns of PV and CB immunoreactivity in the GLd of reptiles and birds (see for references [24]).

In turtles, rotundal PV- and CB-ir neurons project to the ADVRdl (**Figure 2a**, **b**); in pigeons, rotundal neuronal projections terminate in the Ent (**Figure 2c, d**). Geniculate neurons immunoreactive to these proteins project to the dorsolateral cortex in turtles (see details in [23, 31, 32]) and to the Wulst in birds (see Ref. [24]). The density of telencephalic innervation (immunoreactive dotted neuropil) positively correlates with the number of corresponding immunoreactive cells in the projection thalamic nuclei [23, 31, 32].

The prevalence of PV expression in the Rot and CB expression in the GLd in the zebra finch [33, 34] allowed concluding that in birds, the tectofugal system (Rot-Ent) is PV-specific, while the thalamofugal system (GLd-Wulst) is CB-specific. By contrast, in the comparable visual

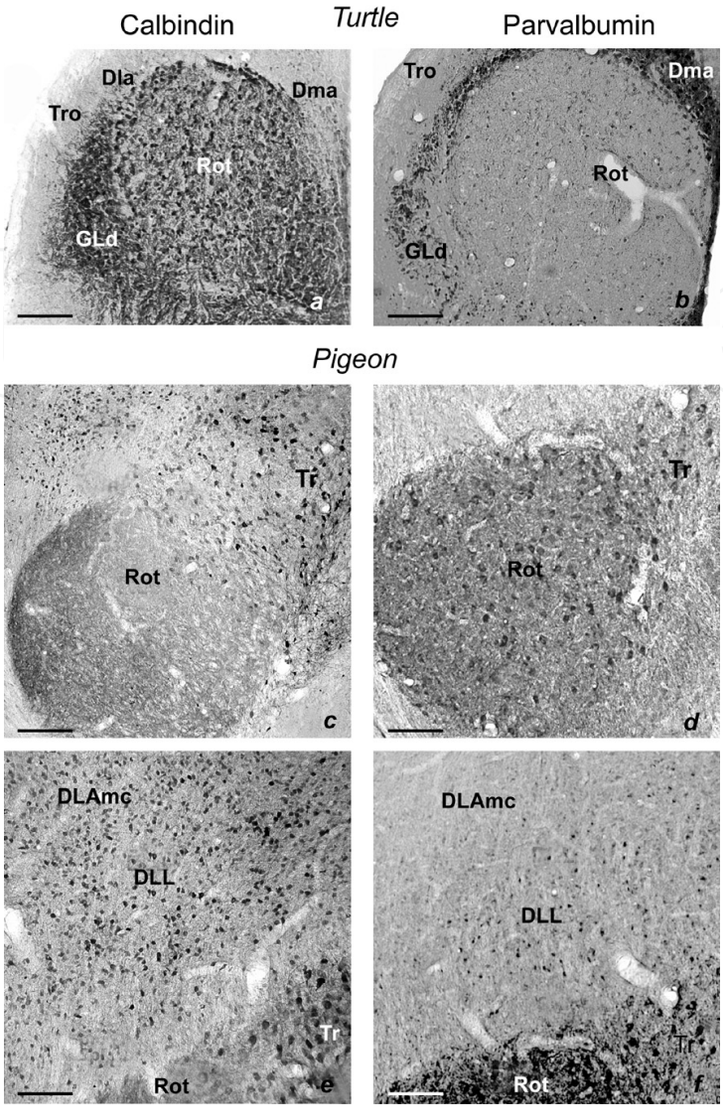

Figure 3. Patterns of parvalbumin and calbindin immunoreactivity in the rot and GLd in turtle and pigeon. Microphotographs of unilateral transverse sections of the thalamus in turtle (a, b) and pigeon (c-f)). Note the prevalence of CB-ir (a) and lesser number of PV-ir (b) cells in the turtle rot in contrast to the prevalence of PV-ir (d) and lesser number of CB-ir cells (c) in the pigeon rot. Both in turtle GLd (a, b) and pigeon GLd—DLAmc, DLL (e, f), prevalence of CB-ir cells (a, e) and lesser number of PV-ir cells (b, f). CB—Calbindin; Dla—N. Dorsolateralis anterior; DLAmc—N. Dorsolateralis anterior magnocellularis; DLL—N. Dorsolateralis anterior lateralis, pars lateralis; Dma—N. Dorsomedialis anterior; GLd—*N. geniculatus* Lateralis, pars dorsalis; PV—Parvalbumin; rot—*N. rotundus*; Tr—*N. triangularis*; And Tro—Tractus opticus. Scale bar: 100 μm.

pathways of mammals [34], the distribution of PV and CB is quite opposite: the extrageniculocortical system (LP/Pulv-extrastriate cortex) is CB-specific. However, the data obtained in the zebra finch cannot be transposed to all avian species because there is a great interspecies variability in the pattern of CaBPr immunoreactivity in the centers of the tecto- and thalamofugal pathways (see Ref. [24]). Similar variability exists in the reptilian thalamic centers of the tecto- and thalamofugal systems, being mainly CB-specific in both cases [23, 24, 31, 32, 35]. Thus, the examples of both similarity and dissimilarity in PV and CB immunoreactivity can be found in homologous visual thalamic centers of reptiles and birds. Here, we disregard

the expression of other CaBPr, although, for example, calretinin has been demonstrated in the visual and auditory thalamic centers in reptiles and birds [23, 32, 34–36].

A study of CaBPr in the thalamus of higher mammals (primates) allowed E. Jones [37] to put forward a hypothesis that PV prevails in the phylogenetically younger, highly specialized lemniscal (core) centers, whereas CB is predominant in the phylogenetically older, less specialized structures (matrix), including the extralemniscal regions (belt/shell) of the sensory nuclei. These findings and the data on CaBPr in the brain structures of nonprimate mammals [37–39], Sauropsida amniotes and anamniote vertebrates (see [24]), led to a conclusion that distribution of different types of PV- and CB-expressing neurons in brain structures depends on the level of phylogenetic development. However, a high variability in the neuronal PV and CB immunoreactivity in the lemniscal parts of the homologous thalamic sensory nuclei in amniotes, including nonprimate mammals, revealed numerous exceptions of the Jones' concept. Altogether, they have led us to conclude that at every stage of phylogenetic history, the specificity to different CaBPr types depends on the functional factor (see discussion in [24]).

2.2. Auditory system

The auditory system in all amniotes contains two parallel pathways such as lemniscal and extralemniscal. Both of them derive from the mesencephalic auditory center, but from its different regions: the lemniscal stems from the core region, while the extralemniscal—from the peripheral belt region. The lemniscal pathway projects to the core (Red+Revm) of the thalamic auditory center nucleus reuniens (Re) in reptiles and to the core (nCe Ov) of the nucleus ovoidalis (Ov) in birds. The extralemniscal pathway projects to the peripheral regions of these nuclei, respectively, to the Revl in reptiles and the Ovl and Ovm in birds. Both pathways have different morphological, neurochemical, and functional characteristics and different targets in the auditory telencephalic regions: the lemniscal—in the core (central area of the ADVRvm in reptiles, L2 in birds), whereas the extralemniscal—in the belt (peripheral area of ADVRvm in reptiles, L1, L3, CMM in birds) [40–48].

The distribution of PV and CB immunoreactivity as well as CO activity was different in the central and peripheral regions of the thalamic auditory centers in turtles and pigeons, reflecting their core-belt organization. In turtles, the core region (Red+Revm) contains both CB- and PV-ir cells as well as a neuropil with prevailing CB immunoreactivity (**Figure 4b, c**), and exhibits high CO activity (**Figure 4a**). The belt region (Revl) is distinguished by a weak immunoreactivity to both proteins and a low CO activity (**Figure 4a–c**). The prevalence of CB-ir cells in Red+Revm positively correlates with a high density of CB-ir neuropil in its projection telencephalic field (ADVRvm) that decreased at the border with the ADVRm (**Figure 4e**). PV immunoreactivity of neuropil in the ADVRvm was far less dense, while CO activity was rather high, but only outside of neuronal clusters (**Figure 4d**).

Pigeons have a more distinct core-belt organization of the thalamic auditory center Ov as compared to the turtle Re. The Ov core region (nCe Ov), like the turtle Red+Revm, contains both CB- and PV-ir cells and neuropil, but with prevailing PV immunoreactivity. The density of dotted PV-ir neuropil and the degree of cell labeling therein were greater (**Figures 5c, d** and **6a**)

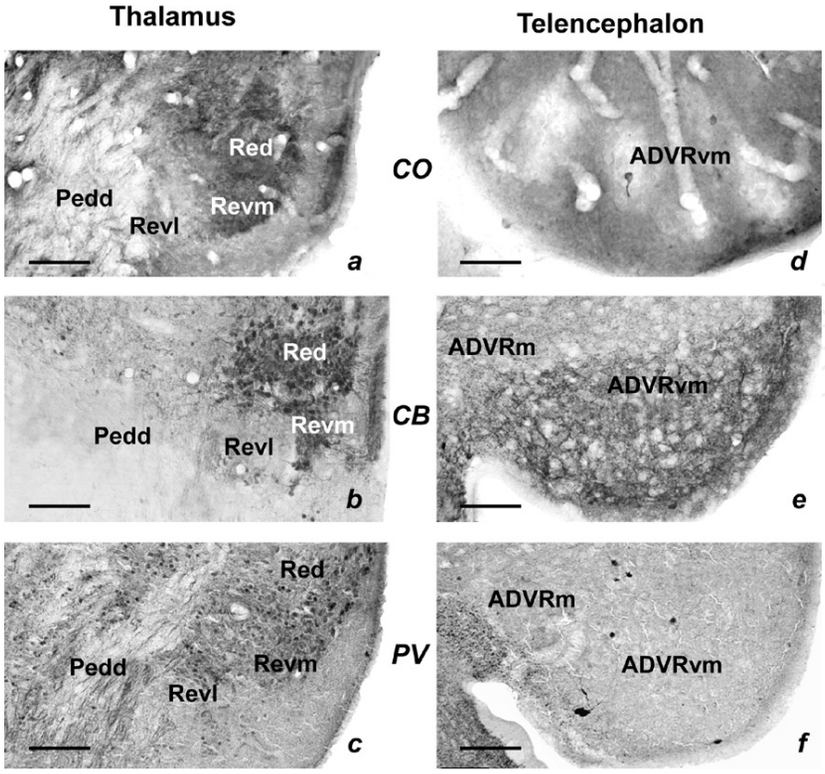

Figure 4. Distribution of calbindin and parvalbumin immunoreactivity and CO activity in the thalamic (re) and telencephalic (ADVRvm) auditory centers in turtle. Transverse unilateral sections at the levels of re (a-c) and ADVRvm (d-f)). A, d—CO activity, b, e—CB, c, f—PV immunoreactivity. Note the highest level of both CB and PV immunoreactivity and CO activity in the red+Revm (core of the re) in contrast to the Revl (belt of the re). Compare the ADVRvm both strongly CB-ir (e) and moderately CO-active (d) terminal neuropil with weakly PV-ir neuropil (f). White areas in d—CO-negative cell clusters. ADVR s– Anterior dorsal ventricular ridge; ADVRm—Medial part of ADVR; ADVRvm—Ventromedial part of ADVR; CB—Calbindin; CO—Cytochrome oxidase; Pedd—Pedunculus dorsalis; PV—Parvalbumin; re—N. Reuniens; red—Re dorsalis; Revl—Re ventrolateralis; and Revm—Re ventromedialis. Scale bar: 100 μm.

than in CB-ir neuropil and its cells (**Figures 5e, f** and **6b**). A high CO activity of neuropil and its cells clearly distinguished the nCe Ov from the peripheral nuclei Ovl and Ovm, where this activity was absent (**Figure 5a, b**).

Like in mammals, the ratio and distribution of CB- and PV-ir neurons in the lemniscal (core) regions of the Re and Ov significantly differ not only across different Sauropsida taxa but also in different species within the same taxonomic group [33, 36, 37, 48, 49]. These interspecies differences relate to peculiarities in the morphofunctional organization of the lemniscal centers in different species, specifically with different localization of brain stem auditory input projections, encoding information about different parameters of sound signaling. Overall, the variability in CaBPr expression in the lemniscal (core) centers is determined by specific mechanisms for processing each auditory modality. Thus, the phenotypic diversity in the CaBPr expression in lemniscal auditory centers may be considered as a result of the complicated interplay between phylogenetic history and ecology-dependent functional specialization with the leading role of the functionally adaptive factor.

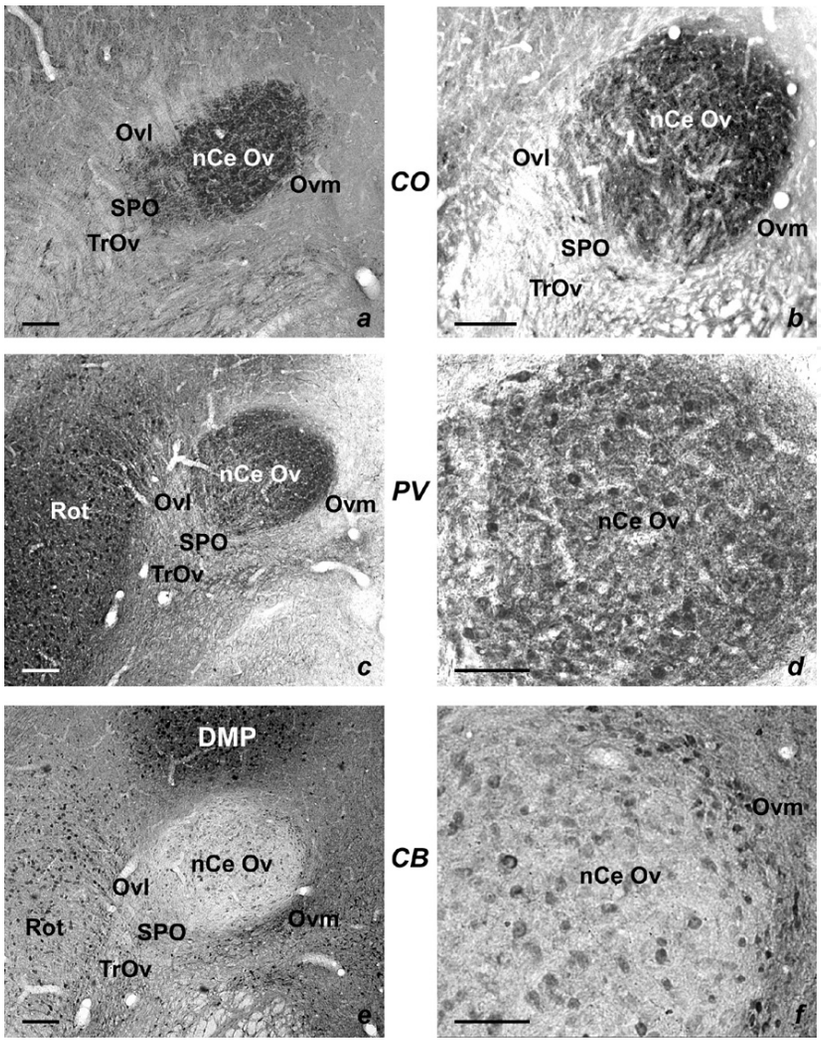

Figure 5. Distribution of calbindin and parvalbumin immunoreactivity and CO activity in the thalamic auditory center (Ov) of the pigeon. Transverse unilateral thalamic sections at the level of the Ov. (a, b)—CO activity located only in the nCe Ov (core). (c, d)—Strong PV immunoreactivity located only in the nCe Ov. (e, f)—CB immunoreactivity located in the nCe Ov, Ovl, and Ovm. Note strongly stained PV-ir and weakly stained CB-ir cells in the nCe Ov (core) in contrast to strongly CB-ir cells in Ovl and Ovm (belt), which are morphologically different from CB-ir cells in the nCe Ov. Note also a high level of CB immunoreactivity in the DMP (e). CB—Calbindin; CO—Cytochrome oxidase; DMP—N. Dorsomedialis posterior; nCe OV—*N. centralis* Ov; Ov—N. Ovoidalis; Ovl—Ov lateralis; Ovm—OV medialis; PV—Parvalbumin; rot—*N. rotundus*; SPO — Nucleus semilunaris parovoidalis; and TrOv—Tractus ovoidalis. Scale bars: 100 μm (a, c, e) and 50 μm (b, d, f).

In the extralemniscal peripheral Ov regions (Ovl and Ovm) of pigeons, a distinct monospecificity to CB was revealed. These nuclei contained only CB-ir cells and dense CB-ir neuropil (**Figures 5e, f** and **6b**), being completely devoid of PV immunoreactivity (**Figures 5c** and **6a**). At the same time, CB-ir cells were more densely packed, strongly labeled, and exhibited a different morphological type as compared to CB-ir cells in the nCe Ov (**Figures 5f** and **6b**). This feature is typical for the belt Ov regions in all the studied avian species and for some belt nuclei in the mammalian auditory thalamic center (nucleus geniculatus medialis) (see for Ref. [48]). Such a strong similarity indicates a high evolutionary conservatism of the extralemniscal auditory thalamic center. It is determined by the fact that peripheral parts of the auditory

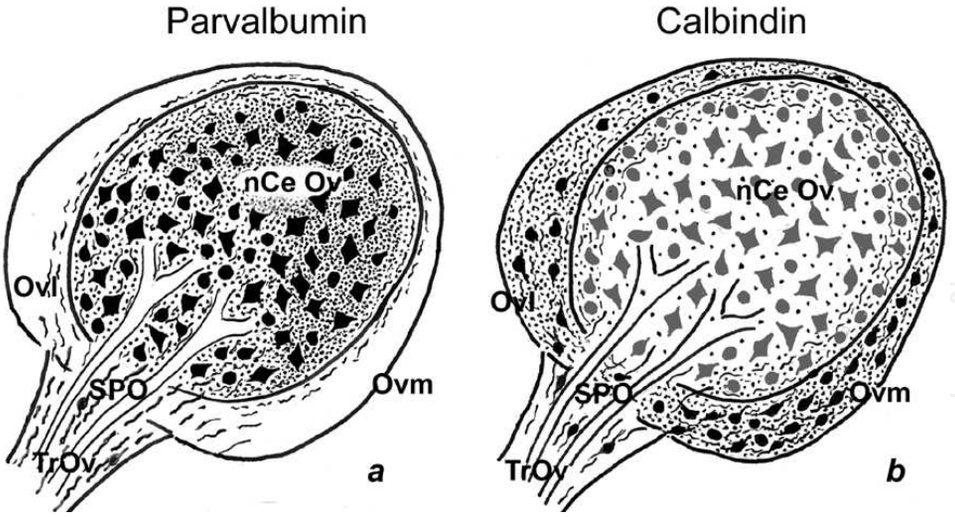

Figure 6. Core-belt organization of the pigeon nucleus ovoidalis. Schematic drawings of transverse sections of the Ov. The core nCe Ov contains both PV-ir (a) and CB-ir (b) cells and dotted neuropil. Note: Strong labeling of PV-ir and weaker labeling of CB-ir cells, high density of PV-ir neuropil, and low density of CB-ir neuropil. Belt Ovl, Ovm, and SPO contain only strongly labeled CB-ir cells and neuropil (b) and devoid of PV-ir cells (a). CB—Calbindin; nCe OV—*N. centralis* Ov; Ov—N. Ovoidalis; Ovl—Ov lateralis; Ovm—OV medialis; PV—Parvalbumin; SPO — Nucleus semilunaris parovoidalis; and TrOv—Tractus ovoidalis.

centers have multiple connections with many other nonauditory, including limbic centers, which provide the involvement of auditory information in different vital functions of the brain, responsible for feeding, reproductive, communicative, and other behaviors served species survival [43, 44, 46, 50].

3. Conclusion

In reptiles and birds (Archosauria), the patterns of calcium-binding protein (PV and CB) expression and metabolic (CO) activity have been shown to differ in distinct areas of the visual and auditory thalamic centers related to different parallel channels within the tecto- and thalamofugal visual pathways as well as the lemniscal (core) and extralemniscal (belt) auditory pathways. No unambiguous positive correlation has been found in the thalamic centers between PV immunoreactivity and high CO activity. The level of metabolic activity is likely to depend on the functional significance of the thalamic centers. The remarkable interspecies variability in PV and CB expression in homologous centers within every phylogenetic lineage appears to result from complicated interrelationships between phylogeny and epigenetic ecology-dependent functional adaptation, reflecting both conservative and plastic traits in their evolutionary development. The patterns of PV and CB immunoreactivity in the thalamic centers of the reptilian and avian visual and auditory systems provide evidence in favor of their homology with the mammalian dorsothalamic projection nuclei and, accordingly, the homology of their projection pallial areas with the mammalian isocortical sensory zones, supporting thereby the Karten's isocortical hypothesis [7, 10].

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