ISSN 0022-0930, Journal of Evolutionary Biochemistry and Physiology, 2017, Vol. 53, No. 2, pp. 143—152. © Pleiades Publishing, Ltd., 2017.
Original Russian Text © N.B. Kenigfest, M.G. Belekhova, T.V. Chudinova, 2017, published in Zhurnal Evolyutsionnoi Biokhimii i Fiziologii, 2017, Vol. 53, No. 2, pp. 127—135.

MORPHOLOGICAL BASICS FOR EVOLUTION OF FUNCTIONS

Distribution of Calcium-Binding Proteins Parvalbumin and Calbindin in the Pigeon Telencephalic Auditory Center

N. B. Kenigfest[a, b]*, M. G. Belekhova[a], and T. V. Chudinova[a]**

[a] *Sechenov Institute of Evolutionary Physiology and Biochemistry, Russian Academy of Sciences, St. Petersburg, Russia*

[b] *Muséum National d'Histoire Naturelle USM-0501, Paris, France*
*kenig51@yahoo.com, **belekhova@yahoo.com

Received April 18, 2016

Abstract—Immunoreactivity for calcium-binding proteins parvalbumin (PV) and calbindin (CB) was studied in the pigeon (*Columba livia*) telencephalic auditory center. All its regions displayed overlapping distribution patterns of PV and CB immunoreactivity, although in the central (L2) vs. peripheral (L1, L3, CMM) layers they were dissimilar. L2 and the inner L1 sublayer (L1i) were distinguished by a higher immunoreactivity of neuropil for both proteins and the presence (in L2) of numerous small densely packed granular-type cells: heavily stained PV-ir and, as a rule, poorly stained CB-ir neurons. In Lli, the number of neurons and the density of neuropil immunoreactive to both proteins decreased. The outer L1 sublayer (L1e) as well as L3 and CMM were characterized by a generally lesser density and irregular distribution of immunoreactive neuropil and a heterogenous repertoire of PV-ir and CB-ir neurons referring to diverse morphological types, with an increased number of large multipolar cells. The differences in PV and CB immunoreactivity among different regions of the pigeon telencephalic auditory center revealed the similarity of the latter to the laminar auditory cortex in mammals.

DOI: 10.1134/S1234567817020070

Key words: telencephalic auditory center, calcium-binding proteins, birds.

Abbreviations: CaBPr—calcium-binding proteins; CB—calbindin; CLM—mesopallium caudolaterale; CMM—mesopallium caudomediale; CO—cytochrome oxidase; DA—tractus dorsoarcopallialis; ir—immunoreactive; MGB—corpus geniculatum mediale; MLD—nucleus mesencephalicus lateralis, pars dorsalis; L—telencephalic auditory field; L2—L central layer; Lam—lamina mesopallialis; L1, L3—L peripheral layers; L1e—L1 outer sublayer; L1i—L1 inner sublayer; nCe—nucleus centralis Ov; NCM—nidopallium caudomediale; Ov—nucleus ovoidalis; Ovl—nucleus lateralis Ov; Ovm—nucleus medialis Ov; PV—parvalbumin; SPO—nucleus semilunaris parovoidalis.

INTRODUCTION

This work continues our studies on expression of calcium-binding proteins (CaBP) in the mesencephalic and thalamic auditory cortices of the pigeon [1, 2]. In the previous study [2], we addressed the distribution of parvalbumin (PV) and calbindin (CV) in the pigeon thalamic auditory center (Ov) and confirmed the core–belt organization of the latter inherent to Ov in all avian species stud-

ied thus far [3–5]. However, alongside with differences in the pattern of immunoreactivity for these proteins in the central (core) and peripheral (belt) Ov regions, we revealed interspecies differences in the PV and CB distribution also in its central region (nCe). In some avian species, this region displays predominantly PV immunoreactivity, lacking almost completely (finches [6–9]) or containing only few CB-ir neurons (chicken [5, 8, 10]), whereas in the pigeon nCe we found neuropil and numerous cells immunoreactive both to PV and CB, with the latter being weaker [2]. In contrast, the peripheral Ov region, which includes in the pigeon periovoidal nuclei (Ov1, Ovm), was distinctive in displaying only CB immunoreactivity, typically for all avian species studied [2, 5–8, 10].

The telencephalic auditory area, nidopallium field L, also consists of the central (core) L2 and peripheral (belt) L1 and L3 regions. A major site of the ovoidal nucleus nCe projections is L2. The layers L1 and L3 receive auditory information mainly from the thalamic peri/parovoidal nuclei (Ov1, Ovm, SPO) and L2 [11–14]. The main auditory field also comprises the medially adjacent caudomedial mesopallium (CMM) receiving projections from L1 and L3 and to a lesser extent from Ov (see [14–16]). The nuclei of the main thalamoreceptive nucleus L, in turn, project to different meso- and nidopallial areas, forming the extensive audio-sensitive field [12–14, 16].

At present, there is a growing interest in studying the organization of the avian telencephalic auditory center in connection with the mutually competitive hypotheses on the evolutionary origin of thalamotelencephalic sensory systems in birds, including the auditory one. Adherents of the "neocortex" hypothesis believe Ov to be a homolog of the mammalian relay auditory nucleus (MGB) and its pallial projection field L a homolog of the auditory neocortex, a dorsal pallium derivative [15, 17–24].

Followers of the "claustroamygdalar" hypothesis homologize Ov with a part of the mammalian intralaminar/posterior thalamus, projecting to the claustral/basolateral region of the amygdala, a ventral pallium derivative. Accordingly, the pallial Ov projection field is considered as homolog of at least its part [25–27]. Although these alternative hypotheses are actively debated, no ultimate solution has been found to support one of them since each has its individual limitation and argumentation.

Because of this, intensive studies are still going on to ascertain the neural organization as well as hodological, neurochemical, embryogenetic and genotypical characteristics of the avian telencephalic auditory center as compared to projection auditory zones in the mammalian cortex. As is known, in mammals the auditory cortex layers are characterized by dissimilar distribution of PV and CB immunoreactivity [28–32]. A study of expression of CaBP, which play a decisive role in neurogenesis, in the avian pallial auditory field can provide additional arguments in favor of one or another hypothesis.

Since previously we examined the distribution of PV and CB immunoreactivity in the pigeon thalamic relay auditory nucleus [2], in the present work these proteins were chosen to be studied in the pigeon thalamic projection field (L and CMM).

MATERIALS AND METHODS

5 pigeons of the same species (*Columba livia*) that were used in our previous work [2] have been employed in the present experiments. The pigeon brain was fixed through transcardial perfusion of deeply anesthetized birds with 4% paraformaldehyde added with 0.1–0.4% glutaraldehyde. Immunolocalization of PV and CB was performed using a conventional avidin–biotin–peroxidase method on frozen free-floating frontal sections with a thickness of 40 μm. Rabbit polyclonal anti-CB IgG (Swant, Switzerland) diluted 1:5000 and mouse monoclonal anti-PV IgG (Sigma, USA) diluted 1:1000 were applied as the first antibodies. Control brain sections treated with the omission of the first antibodies showed no immunocytochemical reaction. In parallel, sections were stained with thionine. For better discrimination between different regions of the auditory filed, we used the sections that were previously stained histochemically for a mitochondrial oxidative enzyme cytochrome oxidase (CO) [33]. The material was analyzed at the light-microscopic level. We used novel nomenclature to denote the avian

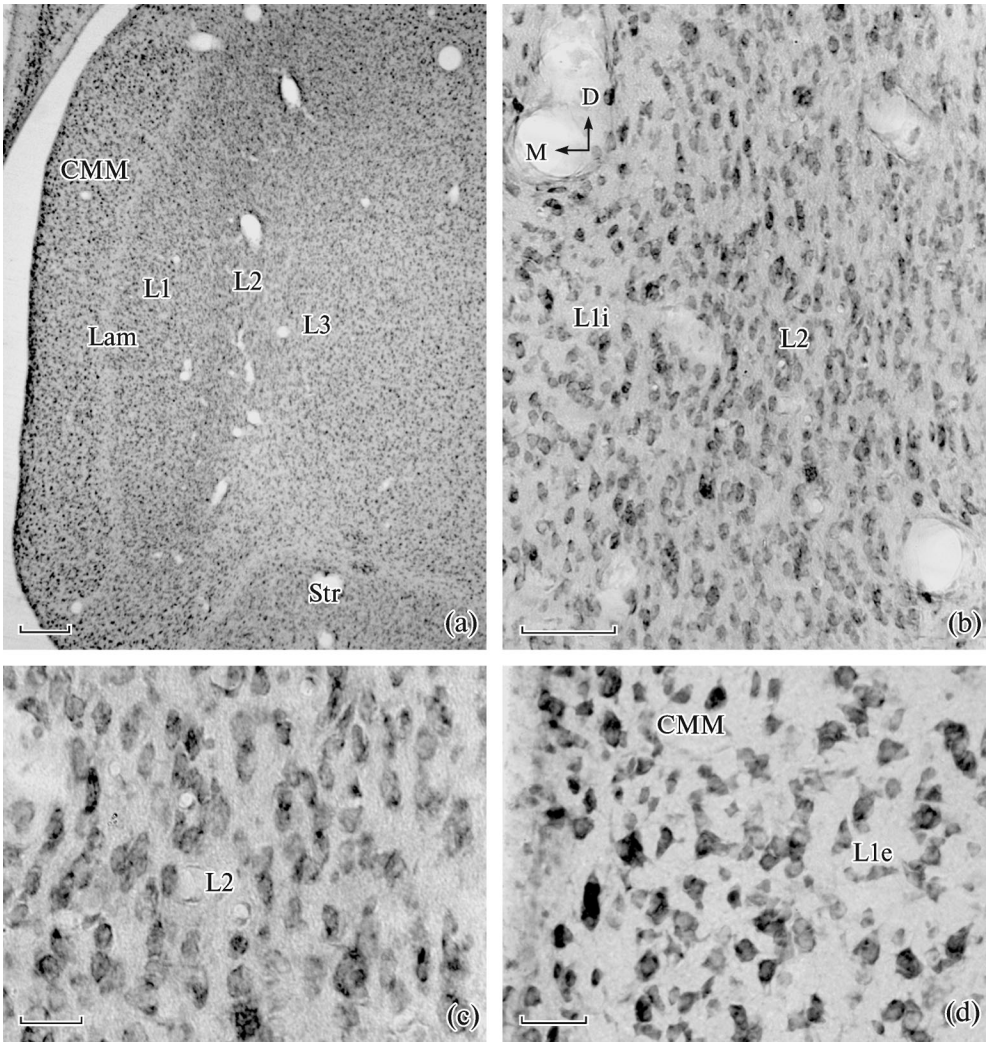

Fig. 1. Cytoarchitectonics of the telencephalic auditory field in the pigeon (Nissl staining). (a) Topography of central (L2) and peripheral (L1, L3, CMM) regions; (b–d) at the higher magnification: (b)—L2 and L1i, (c)—L2, (d)—L1e and CMM. On this and the rest figures: D—dorsal, M—medial sides. Denotations on all figures see in *Abbreviations.* Scale, μm: 200 (a), 100 (b), 25 (c, d).

telencephalic structures [19] and conventional denotations for other brain structures [3, 11].

RESULTS

Cytoarchitectonics. In the pigeon, the vertical layers of the telencephalic auditory center (CMM, L1, L2, L3) reside mediolaterally. Nissl staining shows that field L is separated from CMM by a light mesopallial lamina (Lam) (Fig. 1a). The auditory field layers have a dissimilar cellular repertoire. The narrow layer L2 consists of densely spaced, mainly small rounded/ovoid cells of the granular type and sparse larger cells (Figs. 1b, 1c). In the wider layer L1, its inner sublayer L1i, adjacent to L2, has a similar cellular repertoire, although with a lower spacing density and more numerous larger cells (Fig. 1b). CMM, L1e and L3 contain diffusely scattered cells which are variously shaped and sized, differing generally both from L2 and L1i in a larger number of medium- and large-sized cells as compared to small-sized ones, and this is particularly characteristic of CMM (Fig. 1d).

Parvalbumin immunoreactivity. All the auditory field layers (L1, L2, L3, CMM) were characterized by the presence of PV immunoreactivity, but differed in the repertoire of numerous PV-ir cells and neuropil density (Figs. 2a, 2c, 2d, 2e, 2f). L2

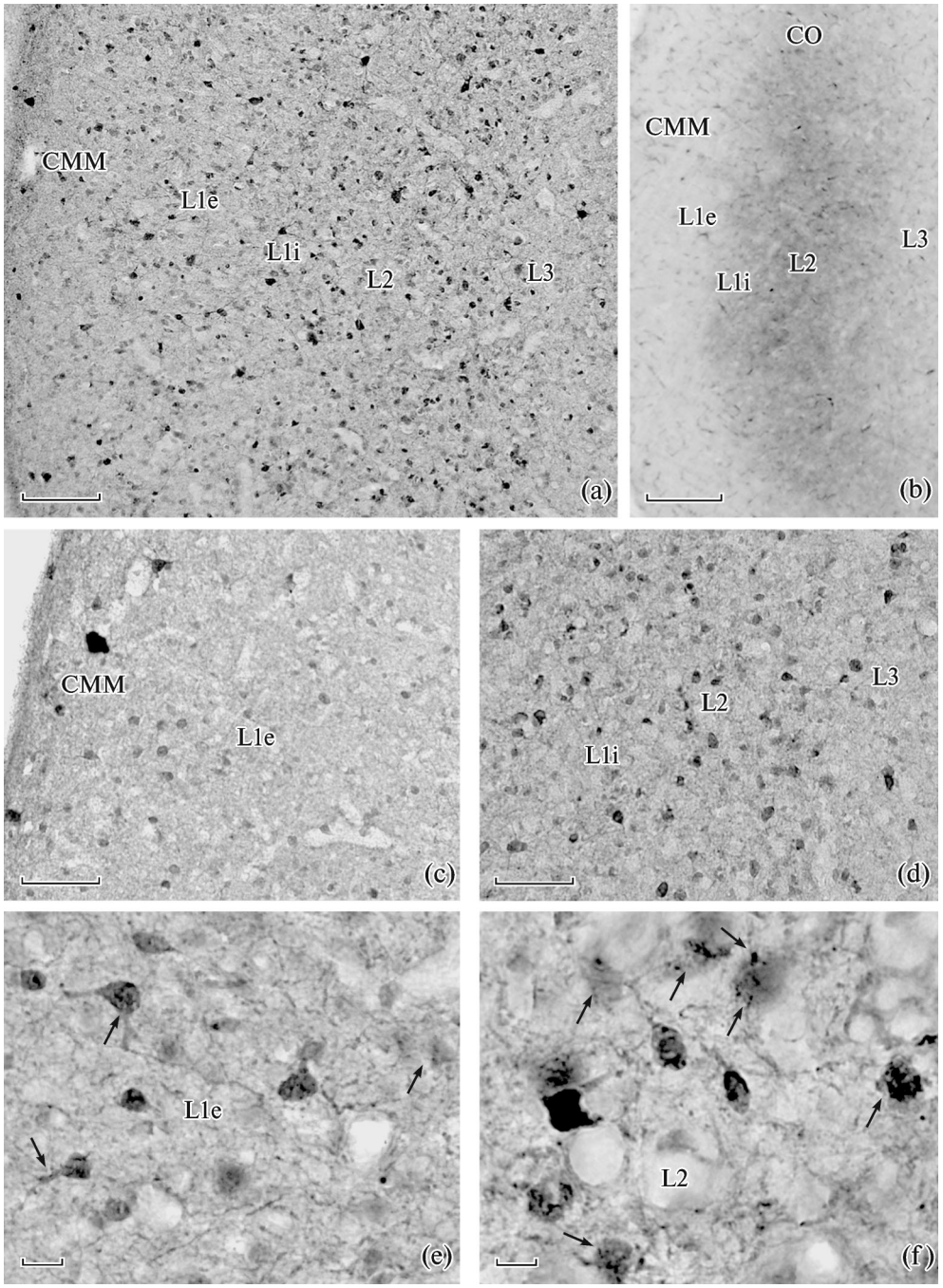

Fig. 2. Distribution of PV immunoreactivity in the pigeon telencephalic auditory field. (a) In central (L2) and peripheral (L1i, L1e, CMM and L3) regions. (b) Activity of cytochrome oxidase (CO) in the same regions of the auditory field; maximum density of neuropil and CO-active neurons in L2. (c–f) PV immunoreactivity at the higher magnification in L1e and CMM (c), in L2, L1i and L3 (d), in L1e (e) and L2 (f). On (e) and (f) see immunoreactive varicose fibers, deriving from cells, and boutons on their bodies and dendrites (*arrows*). Scale, μm: 100 (a–d), 10 (e, f).

contained dense dotted/fibrous PV-ir neuropil and multiple, densely packed and mainly intensely or moderately stained PV-ir cells (Figs. 2a, 2d, 2f). Not always could L2 be distinguished from the adjacent L1i, showing the same pattern of immunoreactivity. L2 identity was supported by the presence of a higher CO activity in neuropil and cells than in L1i and its absence in L1e and L3

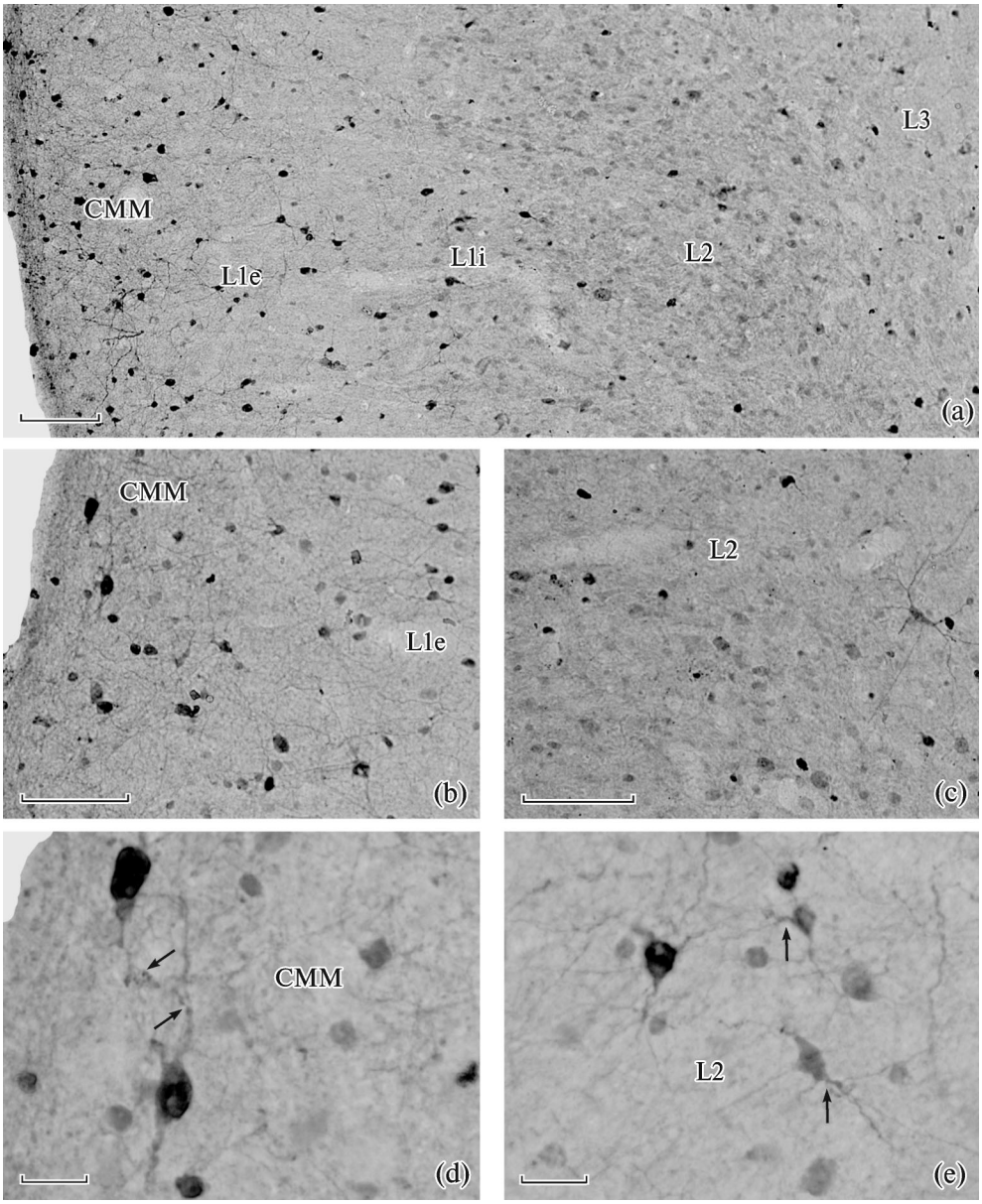

Fig. 3. Distribution of CB immunoreactivity in the pigeon telencephalic auditory field. (a) In central (L2) and peripheral (L1i, L1e, CMM and L3) regions. (b–e) At the higher magnification: in L1e and CMM (b), in L2 (c, e), in CMM (d). On (d) and (e) see boutons, belonging to dendrites and cell bodies (*arrows*). Scale, μm: (a–c) 100, (d–e) 20.

(Fig. 2b). In L2, small and very small rounded/ovoid PV-ir cells of the granular type were predominant (Figs. 2d, 2f). Their density was higher in the ventral region, corresponding to L2a, than in the dorsal (L2b), having different tonopotic organization. Larger and differently shaped PV-ir cells occurred seldom. By their distribution, size and shape, PV-ir neurons coincided with those in L2 stained after Nissl (Fig. 1b, 1c). En passant and terminal boutons of PV-ir fibers were revealed on bodies and processes of PV-ir cells (Fig. 2f). In L1, L3 and CMM, the repertoire of PV-ir neurons was heterogenous and corresponding to that after Nissl staining (Figs. 1b, 1d). L1i, like L2, contained PV-ir neuropil as well as small, rounded and larger PV-ir cells, differing from L2 in their smaller density (Figs. 2a, 2d) and lower CO activity (Fig. 2b). In L1e and L3, the density of immunoreactive neuropil was smaller than in L2 and L1i; variously shaped and sized PV-ir cells were

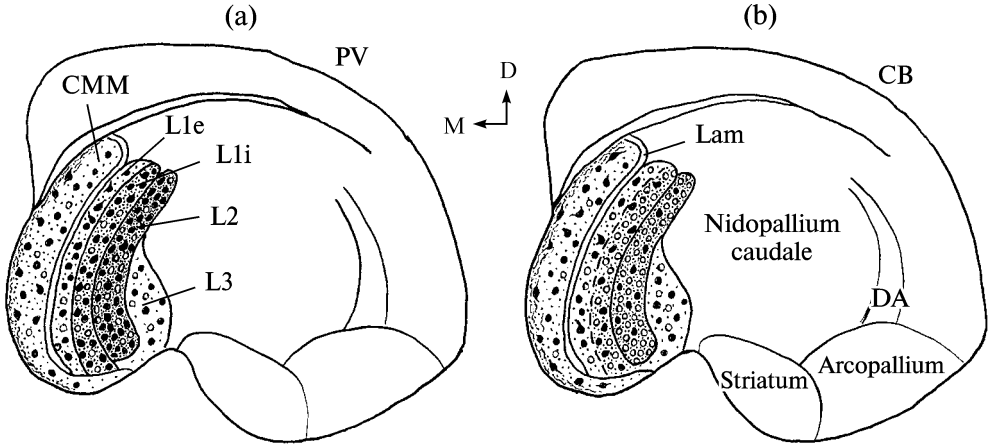

Fig. 4. Diagrammatic representation of the distribution of PV (a) and CB (b) immunoreactivities on the frontal section of the pigeon telencephalon at the medium level. *Small dots and lines*—immunoreactive dotted and fiber-like structures, respectively. *Black symbols and circles*—heavily stained, *white circles*—poorly stained immunoreactive neurons.

diffusely scattered therein with the prevalence of medium- and large-sized ones with often stained dendritic processes (Figs. 2c, 2d, 2e). In the superficial CMM layer, immunoreactive fibers and a densification of neuropil containing sparse large multipolar neurons could be traced (Fig. 2c). L1e, L3 and CMM stood out by the absence of CO activity (Fig. 2b). The bodies and dendritic processes of PV-ie cells in L1e were found to bear terminal boutons (Fig. 2e). The features of the PV immunoreactivity pattern in neurons and neuropil of the pigeon telencephalic auditory field are presented diagrammatically in Fig. 4a.

Calbindin immunoreactivity. Distribution of CB immunoreactivity across the telencephalic auditory field overlaps with that of PV immunoreactivity, although the differences in topography and properties of CB-ir elements in different regions of the field were quite evident (Fig. 3a). Moderately dense CB-ir neuropil filled L2 and L1i. Both these regions contained CB-ir cells (Figs. 3a, 3c). In L2, the densely packed small rounded/ovoid weakly stained cells were predominant; larger and heavily stained multipolar neurons with as stained processes occurred more seldom (Figs. 3a, 3c, 3e). On the bodies and processes of CB-ir cells there were found en passant and terminal boutons of CB-ir fibers (Fig. 3e). Both types of CB-ir cells were also present in L1i, where larger cells were somewhat more while smaller cells less abundant than in L2 (Fig. 3a). A weak staining of most CB-ir cells in L2 and L1i is hardly due to a methodical inaccuracy because CB-ir neurons both in these layers and the peripheral parts of the auditory field as well as in other pallial and subtelencephalic regions of the auditory field displayed in the same experiments a high immunoreactivity, i.e. were heavily stained. In L1e, L3 and CMM, variously shaped and sized CB-ir neurons were scattered diffusely, and among them the large- and medium-sized heavily stained multipolar cells with long multidirectional processes occurred more frequently than in L2 and L1i. Small rounded and mainly poorly stained neurons also occurred in these regions (Figs. 3a, 3b, 3d). Dotted CB-ir neuropil in L1e and L3 had a lower density than in L2 and L1i, which increased in CMM, especially in its superficial region (Figs. 3a, 3b, 3d) where there occurred very large spindle-shaped neurons with bipolar dendritic processes oriented parallel to the outer CMM border and involved in the formation of the superficial CB-ir fibrous plexus (Figs. 3b, 3d). The distributional features of CB immunoreactivity in neurons and neuropil of the pigeon telencephalic auditory center are shown diagrammatically in Fig. 4b.

DISCUSSION

A comparison with other bird species. In other birds, like in pigeons studied in this work, PV and CB immunoreactivities overlap across the entire L-CMM complex with some, not always clear-cut, differences described by different authors.

In the chicken, the density of PV-ir neuropil and cells is more considerable in L2 than in adjacent regions [15]. Another work on the same birds reports a homogeneous distribution of PV- and CB-ir cells and fibers throughout the telencephalic auditory center without obvious differences between the two CaBP in different regions [5]. In finches, PV and CB immunoreactivities are distributed relatively uniformly, with a little higher density of PV-ir neuropil and cells and lower density of CB-ir counterparts in L2 [7]. By our data, the pigeon's main thalamorecipient region of the auditory field L2 is characterized by a high density of mainly small neurons of the granular type, immunoreactive to both CaBP but with a higher immunoreactivity for PV. A weaker immunoreactivity of L2 neuropil to CB than PV corresponds to the CB/PV immunoreactivity ratio in the Ov central region [2]. In L1 and CMM of pigeons and chickens, the sublayers with different patterns of PV and CB immunoreactivity were distinguished [12, 15]. The inner sublayer L1i in pigeons (present data) shares a similarity with L2, whereas the outer sublayer L1e, as well as the inner region of CMM, display a lower density of neuropil and diffusely distributed PV- and CB-ir neurons of various morphotypes. Thus, the complementarity of PV and CB immunoreactivity distribution in the central and peripheral parts of the pallial auditory area in birds is relative, manifesting itself in different neuropil density as well as density and morphotypical repertoire of immunoreactive cells.

A comparison of the telencephalic auditory field in birds with the auditory cortex in mammals. Comparative studies of the telencephalic auditory centers in birds and mammals revealed an exciting resemblance between the auditory cortex layers in mammals and the pallial auditory field regions (L-CMM) in birds. In all the birds studied [5–7, 15, present data], L2 in the normal material contains small PV-expressing neurons of the granular type corresponding to small short-axonal cells situated among the ascending thalamic fibers in the L2 thin lamina [34, 35]. Their morphotype and projections to L2 from the Ov lemniscal (core) region, microconnections with other layers (radial-columnar organization), high density of PV-ir terminals and PV-ie neurons of the granular type, extremely high metabolic activity, and similar pattern of neural activity [6, 11, 12, 15, 18, 33, 36–39, present data] allow the avian L2 to be homologized with the thalamorecipient layer 4 in the mammalian auditory cortex. This idea received support from their genotypical resemblance [15, 18, 20, 21, 23, 24, 40]. The presence in the avian L2 of small poorly stained CB-ir neurons does not rule out this idea, since they are also present, although in a smaller amount, in the layer 4 of the mammalian auditory cortex [29]. Layers L1, CMM and L3 are comparable to supragranular layers (2–3) in the mammalian auditory cortex because their neurons are genotypically similar, receive ascending projections from L2 neurons and have a similar neural activity [15, 18, 23, 24, 38, 39]. In pigeons and other avian species, L1, L3 and CMM contain morphologically diverse types of neurons immunoreactive to PV or CB [5, 7, present data], and this is typical also for the supragranular cortical layers in mammals [28–32]. Neurons with descending extra-thelencephalic connections and access to subthelencephalic auditory centers (Ov, MLd) are actualized in birds via the L1 and L3 projections to the arcopallium; based on this, neurons in the latter are comparable to those in the mammalian cortical layers 5–6. They share a morphological, genotypical and functional resemblance [14, 15, 18, 21–24, 38]. The avian L3 is also compared to the mammalian infragranular layers [37, 39]. In the pigeon CMM, we found very large PV-ir and CB-ir neurons with long processes, but their projections are unknown. Presumably, efferent neurons comparable to those in the mammalian cortical infragranular layers are also present within the boundaries of the main auditory field in birds.

The studies [15, 37–39] provide proof for the functionally specific radial-columnar organization of the avian auditory complex L-CMM similar to that in the mammalian auditory cortex. However, this promising concept, as well as the other above-cited studies, leave unresolved the issue of what mammalian auditory cortex areas, primary (core) or nonprimary (belt), are to be compared with the organization of the pallial auditory field in birds and, accordingly, the PV and CB distribution patterns. In mammals, the primary and secondary (belt) areas of the auditory cortex receive projections from various MGB regions, have different laminar or-

ganization and CaBP distribution, and are distinguished by a level of metabolic activity [28–31, 41]. Their identification with the avian auditory complex layers is still incomplete. In birds, the central L2 layer (core) and peripheral L1, L3 and CMM regions (belt) also receive projections from different Ov regions (respectively, from the central and peripheral), differ in cytoarchitectonics, have different connections, repertoire of PV- and CB-ir neurons and metabolic activity (see Introduction). Due to this, they can be compared with the primary and secondary auditory zones in the mammalian cortex. At the same time, the whole auditory field in birds (L2, L1, L3, CMM) is considered as a primary auditory area [16, 42, 43] with the laminar organization similar to that in mammals (see above). The meso- and nidopallial structures (CMM, CLM, NCM) selectively responding to complex auditory signals, such as species-specific bird songs, are referred to secondary auditory zones in birds due to their hodological and functional characteristics. They are implicated in the memory and learning formation [16, 42, 43]. Whether these secondary (associative) zones also have the laminar organization and what patterns of PV and CB immunoreactivity they have is unknown. In the visual system of birds, the geniculo-hyperpallial and rotundo-entopallial thalamocortical channels are addressed to different pallial structures, which are compared, respectively, with the primary visual and extrastriate cortex in mammals due to similar morphological, hodological, genotypical and functional characters [18, 23, 24, 44]. Yet, there is no ultimate solution of this issue with respect to the pallial auditory area in birds, which has the properties both of primary and belt zones of the auditory cortex in mammals. Considering that the organization of the sensory neocortex and laminar distribution of CaBP vary considerably in different phylogenetic lines of mammals [45], we suggest that during the evolution of amniotes there occurred a convergent and divergent development of homologous cortical fields in mammals and birds, determining their resemblance and differences.

Our data and those reported in the literature [5, 7] on the laminar distribution of PV and CB immunoreactivity in the pallial auditory field of birds, in addition to the above-presented data on the columnar organization of different cell types and connections with the thalamic auditory nucleus Ov as well as on the genotypical characteristics of the auditory field layers argue in favor of the "neocortex" hypothesis. The issue of which auditory area in mammals (primary or secondary) the auditory center (L-CMM field) in birds is comparable to remains open.

Supported by the Program of fundamental studies of the Presidium of the Russian Academy of Sciences no. 19 "Mechanisms of integration of molecular systems in the realization of physiological functions. Integration of regulatory influences in providing functions of an organism".

REFERENCES

1. Belekhova, M.G., Kenigfest, N.B., Chudinova, T.V., and Vesselkin, N.P., Distribution of calcium-binding proteins parvalbumin and calbindin in mesencephalic auditory center in pigeons, *Dokl. RAN,* 2016, vol. 466, pp. 361–365.
2. Belekhova, M.G., Chudinova, T.V., and Kenigfest, N.B., Distribution of calcium-binding proteins parvalbumin and calbindin in the thalamic auditory center in pigeons, *J. Evol. Biochem. Physiol.,* 2016, vol. 52, pp. 482–489.
3. Durand, S.E., Tepper, J.M., and Cheng, M.F., The shell region of the nucleus ovoidalis: a subdivision of avian auditory thalamus, *J. Comp. Neurol.*, 1992, vol. 323, pp. 495–518.
4. Zeng, S., Zhang, X., Peng, W., and Zuo, M.X., Immunohistochemistry and neural connectivity of the Ov shell in song-bird and their evolutionary implications, *J. Comp. Neurol.*, 2004, vol. 470, pp. 192–209.
5. Zeng, S.J., Lin, Y.T., Yang, L., Zhang, X.W., and Zuo, M.X., Comparative analysis of neuronogenesis between core and shell regions in the chick (*Gallus gallus domesticus*), *Brain Res.*, 2008, vol. 1216, pp. 24–37.
6. Braun, K., Scheich, H., Schachner, M., and Heizmann, C.W., Distribution of parvalbumin, cytochrome oxidase activity and 14 C-2-desoxyglucose uptake of the zebra finch. I. Auditory and vocal motor systems, *Cell Tissue Res.*, 1985, vol. 240, pp. 101–115.
7. Braun, K., Scheich, H., Heizmann, C.W., and Hunziker, W., Parvalbumin and calbindin-D-28k immunoreactivity as developmental markers of auditory and vocal motto nuclei of the zebra finch, *Neurosci.*, 1991, vol. 40, pp. 853–869.
8. Heizmann, C.W. and Braun, K., Calcium binding

proteins. Molecular and functional aspects, *The Role of Calcium in Biological Systems*, Roca Raton, FL, CRC Press Inc., 1990, pp. 21–65.
9. Pinaud, R., Saldanha, C.J., Wynne, R.D., Lovell, P.V., and Mello, C.V., The excitatory thalamo-cortical projection within the song control system of zebra finches is formed by calbindin-expressing neurons, *J. Comp. Neurol.*, 2007, vol. 504, pp. 601–618.
10. Roth, J., Baetens, D., Norman, A.W., and Garcia-Segura, L.M., Specific neurons in chick central nervous system stained with antibody against chick intestinal vitamin D-dependent calcium binding protein, *Brain. Res.*, 1981, vol. 222, pp. 452–457.
11. Karten, H.J., The ascending auditory pathway in the pigeon (*Columba livia*) II. Telencephalic projections of the nucleus ovoidalis thalami, *Brain Res.*, 1968, vol. 11, pp. 134–163.
12. Wild, J.M., Karten, H.J., and Frost, B.J., Connections of the auditory forebrain in the pigeon (*Columba livia*), *J. Comp. Neurol.*, 1993, vol. 337, pp. 32–62.
13. Vates, G.E., Broome, B.M., Mello, C.V., and Nottebohm, F., Auditory pathways of caudal telencephalon and their relation to the song system of adult male zebra finch, *J. Comp. Neurol.*, 1996, vol. 366, pp. 613–642.
14. Elliott, T.M. and Theunissen, F.E., *The Avian Auditory Pallium. Auditory Cortex*, Springer, New York and oth., 2011, pp. 429–443.
15. Wang, Y., Brzozowska-Precht, H.J., and Karten, H.J., Laminar and column auditory cortex in avian brain, *PNAS*, 2010, vol. 107, pp. 12 676–12 681.
16. Prather, J.F., Auditory signal processing in communication: perception and performance of vocal sounds, *Hearing Res.*, 2013, vol. 305, pp. 144–155.
17. Karten, H.J., The organization of the avian telencephalon and some speculations on the phylogeny of the amniote telencephalon, *Ann. NY Acad. Sci.*, 1969, vol. 167, pp. 164–179.
18. Karten, H.J., Vertebrate brains and evolutionary connections: on the origins of the mammalian "neocortex", *Phil. Trans. Roy. Soc. B.*, 2015, vol. 370.0060.
19. Reiner, A., Yamamoto, K., and Karten, H.J., Organization and evolution of the avian brain, Anat. Rec., 2005, vol. 287 A, pp. 1080–1102.
20. Jarvis, E.D., Güntürkün, O., Bruce, L.L., Csillag, A., Karten, H.J., Kuenzel, W., Medina, L., et al., Avian brains and a new understanding of vertebrate brain evolution, *Nat. Rev. Neurosci.*, 2005, vol. 6, pp. 151–159.
21. Wild, J.M. and Krutzfeldt, N.O.E., Neocortical-like organization of avian auditory cortex, *Brain Behav. Evol.*, 2010, vol. 76, pp. 89–92.
22. Butler, A.N., Reiner, A., and Karten, H.J., Evolution of amniote pallium and the origins of mammalian neocortex, *Ann. N.Y. Acad. Sci.*, 2011, vol. 1225, pp. 14–27.
23. Dugas-Ford, J., Powell, J.J., and Ragsdale, C.W., Cell-type homologies and the origin of the neocortex, *PNAS*, 2012, vol. 109, pp. 16974–16979.
24. Reiner, A., You are who you talk with—a commentary on Dougas-Ford et al., PNAS, 2012, *Brain Behav. Evol.*, 2013, vol. 81, pp. 146–149.
25. Bruce, L.L., Kornblum, H.I., and Seroogy, K.B., Comparison of thalamic populations in mammals and birds: expression of ErbB4 mRNA, *Brain Res. Bull.*, 2002, vol. 57, pp. 455–461.
26. Puelles, L., Thoughts on the development, structure and evolution of the mammalian and avian telencephalic pallium, *Phil. Trans. Roy. Soc. B*, 2001, vol. 356, pp. 1583–1598.
27. Striedter, G.F., *Principles of Brain Evolution*, University of California Press, Irvine, 2005.
28. De Venecia, R.K., Smelser, C.B., and McMullen, N.T., Parvalbumin is expressed in a reciprocal circuit linking the medial geniculate body and auditory neocortex in the rabbit, *J. Comp. Neurol.*, 1998, vol. 400, pp. 349–362.
29. Cruikshank, S.J., Killackey, H.P., and Metherate, R., Parvalbumin and calbindin are differently distributed within primary and secondary subdivisions of the mouse auditory forebrain, *Neurosci.*, 2000, vol. 105, pp. 553–569.
30. Chiry, O., Tardif, E., Magistretti, P.J., and Clarke, S., Patterns of calcium-binding proteins support parallel and hierarchical organization of human auditory areas, *Eur. J. Neurosci.*, 2003, vol. 17, pp. 397–410.
31. Desegent, S., Boire, D., and Ptito, M., Distribution of calcium binding proteins in visual and auditory cortices of hamster, *Exp. Brain Res.*, 2005, vol. 163, pp. 159–172.
32. Wong, P. and Kaas, J.H., Architectonic subdivisions of neocortex in Galago (*Otolemur garnetti*), *Anat. Rec.*, 2010, vol. 293, pp. 1033–1069.
33. Belekhova, M.G., Chudinova, T.V., and Kenigfest, N.B., Metabolic activity of thalamic and telencephalic auditory centers in pigeons, *Zh. Evol. Biokhim. Fiziol.,* 2009, vol. 45, pp. 512–517.
34. Fortune, E.S. and Margoliash, D., Cytoarchitectonic organization and morphology of cells of the field L complex in male zebra finches (*Taenopigia guttata*), *J. Comp. Neurol.*, 1992, vol. 325, pp. 388–404.
35. Saini, K.D. and Leppelsack, H.J., Cell types of the

auditory neostriatum of the starling (*Sturnus vulgaris*), *J. Comp. Neurol.*, 1981, vol. 198, pp. 209–229.
36. Brauth, S.E., Investigation of central auditory nuclei in the budgerigar with cytochrome oxidase histochemistry, *Brain Res.*, 1990, vol. 508, pp. 142–146.
37. Bosman, C.A. and Aboitiz, F., Functional constraints in the evolution of brain circuits, *Front. Neurosci.*, 2015, vol. 9, p. 303.
38. Calabrese, A. and Woolley, S.M.N., Coding principles of the canonical cortical microcircuits in tha avian brain, *Proc. Natl. Acad. Sci. USA*, 2015, vol. 112, pp. 3517–3522.
39. Harris, K.D., Cortical computation in mammals and birds, *Proc. Natl. Acad. Sci.*, 2015, vol. 112, pp. 3184–3185.
40. Atoji, Y. and Karim, M.R., Expression of the neocortical marker RORβ in the entopallium and Field L2 of adult chicken, *Neurosci. Lett.*, 2012, vol. 521, pp. 119–124.
41. Jones, E.G., Viewpoint: the core and matrix of thalamic organization, *Neurosci.*, 1998, vol. 85, pp. 331–345.
42. Pinaud, R. and Terleph, T.A., A songbird forebrain area potentially involved in auditory discrimination and memory formation, *J. Biosci.*, 2008, vol. 33, pp. 145–155.
43. Meliza, C.D. and Margoliash, D., Emergence of selectivity and tolerance in the avian auditory cortex, *J. Neurosci.*, 2012, vol. 32, pp. 15158–15168.
44. Krűtzfeldt, N.O. and Wild, M., Definition and novel connections of the entopallium in the pigeon (*Columba livia*), *J. Comp. Neurol.*, 2005, vol. 490, pp. 40–56.
45. Hof, P.R., Glezer, T.T., Conde, F., Flagg, R.A., Rubin, M.B., Nimchinsky, E.A., Vogt, and Weisenhorn, D.M., Cellular distribution of the calcium-binding proteins parvalbumin, calbindin, and calretinin in the neocortex of mammals: phylogenetic and developmental patterns, *J. Chem. Neuroanat.*, 1999, vol. 16, pp. 77–116.