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Brain Research Bulletin 75 (2008) 348–355

BRAIN RESEARCH BULLETIN

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Research report

Calcium-binding proteins label functional streams of the visual system in a songbird

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Received 2 August 2007; accepted 17 October 2007
Available online 20 November 2007

Abstract

The vertebrate nervous system has been shown to contain high concentrations of intracellular calcium-binding proteins, each of them with a restricted expression pattern in specific brain regions and specific neuronal subpopulations. Using immunohistochemical staining techniques, we analyzed the expression pattern of calbindin, calretinin and parvalbumin in visual brain areas of a songbird species, the zebra finch (*Taeniopyga guttata*). Here we show that the analyzed proteins are expressed in a complementary fashion within different brain substructures generally corresponding to functional subpathways of the avian visual system. In detail, calbindin is expressed in the brain structures that belong to the thalamofugal pathway, whereas parvalbumin-positive neurons are found in the brain structures that are part of the tectofugal visual pathway. Originally, the expression of calcium-binding proteins has been associated with specific morphological or neurochemical criteria of neurons. Our results suggest that their expression pattern also indicates a functional segregation of brain substructures linked to vision in the zebra finch brain. As the selective labeling of functional streams has also been shown for the visual system in mammalian species, function-selective expression of calcium-binding proteins might be a general feature of vertebrates.

Keywords: Calbindin; Calretinin; Parvalbumin; Tectofugal; Thalamofugal; Visual pathway

1. Introduction

In the central nervous system, information originating from the sensory organs is processed in a network of brain areas adapted to carrying out particular processing tasks, such as the processing of visual, auditory, or somatosensory information. Each of these functional networks consist of numerous areas across the brain that are heavily interconnected. Even though these networks converge in various multimodal areas, the sensory pathways retain a certain degree of separateness throughout their extent that may span large parts of the central nervous system. For instance, the visual system includes structures in mesencephalic [optic tectum, nucleus of the basal optic root (nBOR), isthmic system], diencephalic [retina, thalamic geniculate complex (Gld), nucleus rotundus (Rt)], and telencephalic [nidopallium, hyperpallium] brain regions [13,12,41]

Ca^{2+} acts as a secondary messenger to translate external signals into intracellular information and thus is involved in the regulation of various cell functions, among them

Abbreviations: APH, area parahippocampalis; CB, cerebellum; E, entopallium; DLA, nucleus dorsolateralis anterior thalami; DLAmc, nucleus dorsolateralis anterior thalami, pars magnocellularis; DLL, nucleus dorsolateralis anterior, pars lateralis; FPL, fasciculus prosencephali longitudinalis; H, hyperpallium; HA, hyperpallium apicale; HD, hyperpallium densocellulare; HL, hyperstriatum laterale; Hp, hippocampus; IHA, interstitial nucleus of the HA; LdOPT, nucleus lateralis dorsalis nuclei optici principalis thalami; LMD, lamina medullaris dorsalis; LSt, lateral striatum; MD, mesopallium dorsale; MO, medulla oblongata; MSt, medial striatum; MV, mesopallium ventrale; nMOT, nucleus marginalis tractus optici; OM, tractus occipitomesencephalicus; OT, optic tectum; Rt, nucleus rotundus; SPC, nervus superficialis parvocellularis; SpRt, nucleus suprarotundus; St, striatum; T, telencephalon; Tel, telencephalon; TrO, tractus opticus; TSM, tractus septo-mesencephalicus.

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doi:10.1016/j.brainresbull.2007.10.029

synaptic transmission. Translation into an intracellular signal for instance requires the presence of calcium-binding proteins (CaBPs), which have multiple cellular functions (e.g. calcium buffering/messenger target). CaBPs belong to a family of low molecular weight proteins characterized by often homologous primary structures containing polypeptide folds for the acceptance of incoming Ca^{2+}. Their restricted expression in neuronal subpopulations of the central and peripheral nervous system has been extensively described in many vertebrate and invertebrate species. Although the functional meaning of a differential expression of CaBPs is not clear, CaBPs have been used to delineate cell types and to analyze neuronal circuits with double labeling techniques since CaBP stainings tend to reveal the detailed morphology of the neurons [1,6,8,48].

However, in addition to labeling individual cell types, certain CaBPs might also characterize networks of brain areas that form functional units. In the mammalian nervous system, antibodies against various CaBPs have been shown to selectively label defined cell groups, particularly within visual brain areas. There, certain CaBPs show a complementary laminar and columnar distribution generally corresponding to either the geniculocortical or the extrageniculocortical stream [9,46]. In the avian thalamofugal pathway, which is suggested to correspond to the mammalian geniculostriate pathway [42], retinofugal fibers curve into the contralateral GLd located in the dorsolateral thalamus [12]. From here, bilateral projections lead to the visual wulst of the anteriodorsal forebrain [12,18] with the relative amount of ipsi- and contralaterally projecting fibers depending on the degree of stereoscopic vision (frontal-eyed birds [3]; lateral-eyed birds [14]). In contrast, in the tectofugal pathway, retinofugal fibers invade the contralateral optic tectum. From here information is sent bilaterally to the thalamic Rt [5,25,22,30], which itself sends efferents to the ipsilateral telencephalic entopallium [4,19,26]. Entopallial neurons project to the surrounding entopallial belt area, from where intratelencephalic projections lead to several forebrain structures [26]. It is however not clear whether the above mentioned differential expression of CaBPs in mammals is a coincidence, a general mammalian or even a general vertebrate pattern. Therefore, the aim of this study was to investigate, whether CaBPs can be used as markers for functional visual streams in birds by analyzing the expression of three CaBPs [calbindin (CB), calretinin (CR) and parvalbumin (PV)] in visual brain components of the most commonly used songbird species in neurobiological studies, the zebra finch (*Taeniopyga guttata*), which we also use as the non-migratory control species in our studies of light-mediated magnetic compass orientation mechanisms e.g. [28,35,36].

2. Material/methods

All animal procedures used in this study were approved by local and national authorities for the use of animals in research. For immunohistochemical detection of CaBP-immunoreactive cells, five adult male zebra finches, obtained from a local breeder, were transcardially perfused with 0.12 M phosphate buffered saline (PBS) followed by 4% paraformaldehyde (PFA) in PBS. After postfixation and cryoprotection, brains were cryosectioned (Leica 1850, Solms, Germany) in the frontal plane in six series at 40 μm.

Table 1
Relative amounts of immunoreactivity in visual brain regions

	Calbindin		Calretinin		Parvalbumin	
	Somata	Neuropil	Somata	Neuropil	Somata	Neuropil
Thalamus						
DLAmc	++	++	++	++	–	–
DLL	+	+	++	++	–	–
LdOPT	+	+	++	++	–	–
nMOT	o	+	++	++	–	–
Rt	–	–	–	o	++	++
SpRt	o	+	++	++	–	–
Entopallium	–	–	o	o	+	++
Hyperpallium						
HA	+	++	o	++	o	+
HD	+	–	o	++	o	+
HL	++	++	+	+	o	+
IHA	+	+	o	o	+	+

Intensity of immunosignal is classified in: (–), no ir; (o), low; (+), moderate; (++), high. Respective immunosignals for tectal layers are depicted in Fig. 2D.

Staining procedures were as described previously [17]. In brief, parallel series of brain slices were stained free-floating using the immuno-ABC-technique. Each incubation step was followed by rinsing sections in PBS. Endogenous peroxidases were inactivated by incubation with 0.3% hydrogen peroxide followed by blocking unspecific binding sites with 10% normal serum dissolved in PBS containing 0.3% Triton-X100 (PBS-T, Sigma, Deissenhofen, Germany). Whole series were incubated with one of the following primary antibodies overnight: polyclonal rabbit calbindin (Swant, Bellinzona, Switzerland), 1:1000; polyclonal rabbit calretinin (Swant, Bellinzona, Switzerland), 1:1000; monoclonal mouse parvalbumin (Sigma, Deisenhofen, Germany), 1:500 in PBS-T). Thereafter, sections were sequentially incubated with biotinylated secondary antibodies and avidin-coupled peroxidase-complex (Vector ABC Elite Kit, Vector Laboratories, Burlingame, CA). Peroxidase-activity was detected using a 3′3-diaminobenzidine (DAB; Sigma, Deisenhofen, Germany) reaction, modified by using β-D-glucose/glucose-oxidase (Sigma, Deisenhofen, Germany; [43]). After enough reaction product had formed, slices were transferred into PBS. Sections were mounted on gelatinized slides, dehydrated and embedded in Entellan (Merck, Darmstadt, Germany).

Images presented in this article were taken with a digital camera (Leica DFC 320, Solms, Germany) mounted to a stereomicroscope (Leica M, Leica IM 50, Solms, Germany). Schematic drawings, labeling and layout were done using Photoshop 6.0/Illustrator 10.0 (Adobe Systems, Mountain View, CA). Neuroanatomical structures were identified and named using brain atlases of the chicken [27], pigeon [23] and canary [44].

3. Results

CB-, CR- and PV-immunoreactive cells were mapped in visual brain areas of the mesencephalon (optic tectum, Fig. 1A and B; Fig. 2A–D), diencephalon (Gld, Rt, Fig. 1A and C; Fig. 2E–H) and telencephalon (entopallium, Fig. 1A and D; Fig. 3A–D; visual wulst, Fig. 1A and E; Fig. 3E–H) of zebra finches (*Taeniogyga guttata*). Each of the proteins analyzed showed a unique expression pattern restricted to neuronal subpopulations or functional brain units (e.g. layers, brain nuclei) within the known visual relay centers. Relative intensities of immunosignal are summarized in Table 1.

In the optic tectum, immunohistochemical stainings revealed unique expression patterns for each type of CaBP that generally corresponded to tectal layers. In detail, CB-ir neurons were confined to layers 2–4, 5, 8 and 10–13 with the majority of neurons found in layers 8 and 10–13. CB-ir fibers were detected in

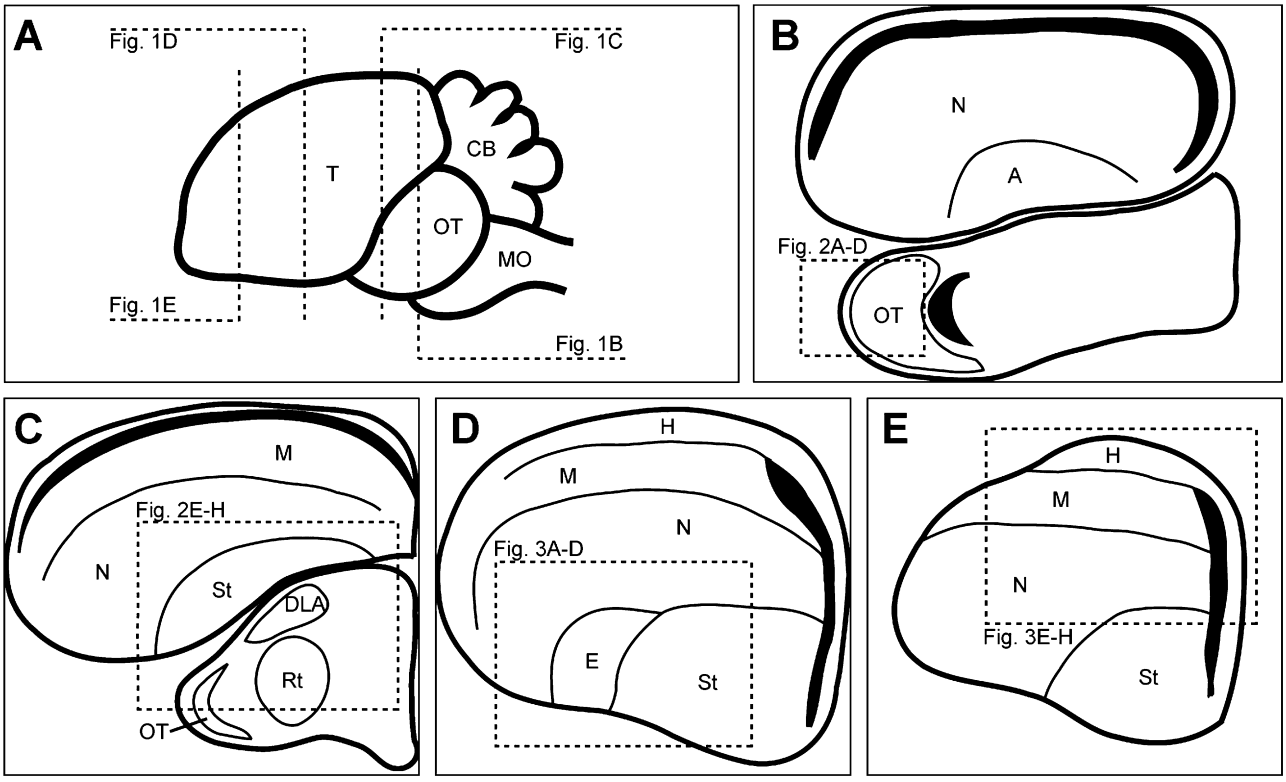

Fig. 1. Anatomical location of brain structures analyzed. (A) Schematic drawing of a zebra finch brain in side view. Frontal section levels are indicated as dotted lines. (B–E): Frontal brain sections at the level of the optic tectum (B), the thalamus (C), the entopallium (D) and the hyperpallium (E). Locations of magnified details depicted in Figs. 2 and 3 are indicated with dotted frames.

layers 3 and 5, putatively resembling the horizontally oriented arborizations of large intrinsic CB-ir neurons in layer 5 [31], and layer 13 stemming from a subpopulation of large multipolar CB-immunopositive neurons located in the same layer (Fig. 2A and D). CR-ir neurons were found in layers 2–5, 8 and 10–13 with dendrites densely covering layers 4, 5, 8 and 13. Radial processes of small granular neurons within layer 8 ascended into retinorecipient layer 5 (Fig. 2B and D). In contrast, PV-ir neurons were found in layers 2–4, 6, 8–10 and 13 with a dense fiber network spanning the whole optic tectum basal to layer 6, except for layer 7. Radial processes extended into superficial layer 4, originating from small neurons in layer 9 and large spindle-shaped bipolar neurons in layers 10 (Fig. 2C and D).

In the lateral geniculate complex, CB-ir neurons covered all retinorecipient substructures, i.e. the Nucleus dorsolateralis anterior thalami, pars magnocellularis (DLAmc), Nucleus dorsolateralis anterior thalami, pars lateralis (DLL), Nucleus lateralis dorsalis nuclei optici principalis thalami (LdOPT), Nucleus suprarotundus (SpRt) and the Nucleus marginalis tractus optici (nMOT) with the majority of neurons being located in dorsal portions of the DLL and the DLAmc. Additionally, fibers within all substructures and the neighboring Fasciculus prosencephali lateralis (FPL) were labeled with antibodies against CB (Fig. 2E and H). CR-ir neurons and fibers had a very comparable distribution, with even stronger labeling of all the structures where CB-ir was observed (Fig. 2F and H). In stark contrast to these distributions, PV-ir neurons and fibers were completely absent in the Gld (Fig. 2G and H).

The Nucleus rotundus is the main tectorecipient brain unit in the diencephalon and completely lacked CB-immunoreactive neurons and dendrites (Fig. 2E and H). Few fibers within the Rt exhibited immunoreactivity against CR (Fig. 2F and H). In contrast, strong labeling against PV was observed in neurons within the Rt with a ventrally decreasing gradient (Fig. 2G and H).

In the entopallium, CB-immunoreactive neurons were completely absent (Fig. 3A and D). In contrast, CR-ir was observed in lateral portions at the ento-/nidopallial boundary (Fig. 3B and D). Immunoreactivity against PV was observed in the whole entopallium with a strongly ascending gradient towards lateral portions (Fig. 3C and D; [26]), which represent the main subregion of afferents from the rostral part of the Rt [19]. Particularly, the rostral Rt portion, as described above, exhibits strong immunoreactivity against PV as well (Fig. 2G and H).

The visual wulst, from outwards to inwards, is subdivided into hyperpallium apicale (HA), interstitial nucleus of the HA (IHA), hyperpallium intercalatum (HI) and hyperpallium densocellulare (HD) [40]. Only IHA and HD have been shown to receive direct input from visual nuclei of the Gld [24,48]. CB-immunoreactive neurons were found in all wulst compartments. Strong additional fiber labeling was observed in HA, IHA and the laterally flanking lateral hyperpallium (HL, Fig. 3E and H). CR expression was observed in HA, IHA, HD and HL with intense fiber labeling in HD and HL subdivisions (Fig. 3F and H). PV-immunoreactivity was found in HD, HL, and to a lesser degree in the IHA. PV-ir dendrites were distributed similarly (Fig. 3G and H).

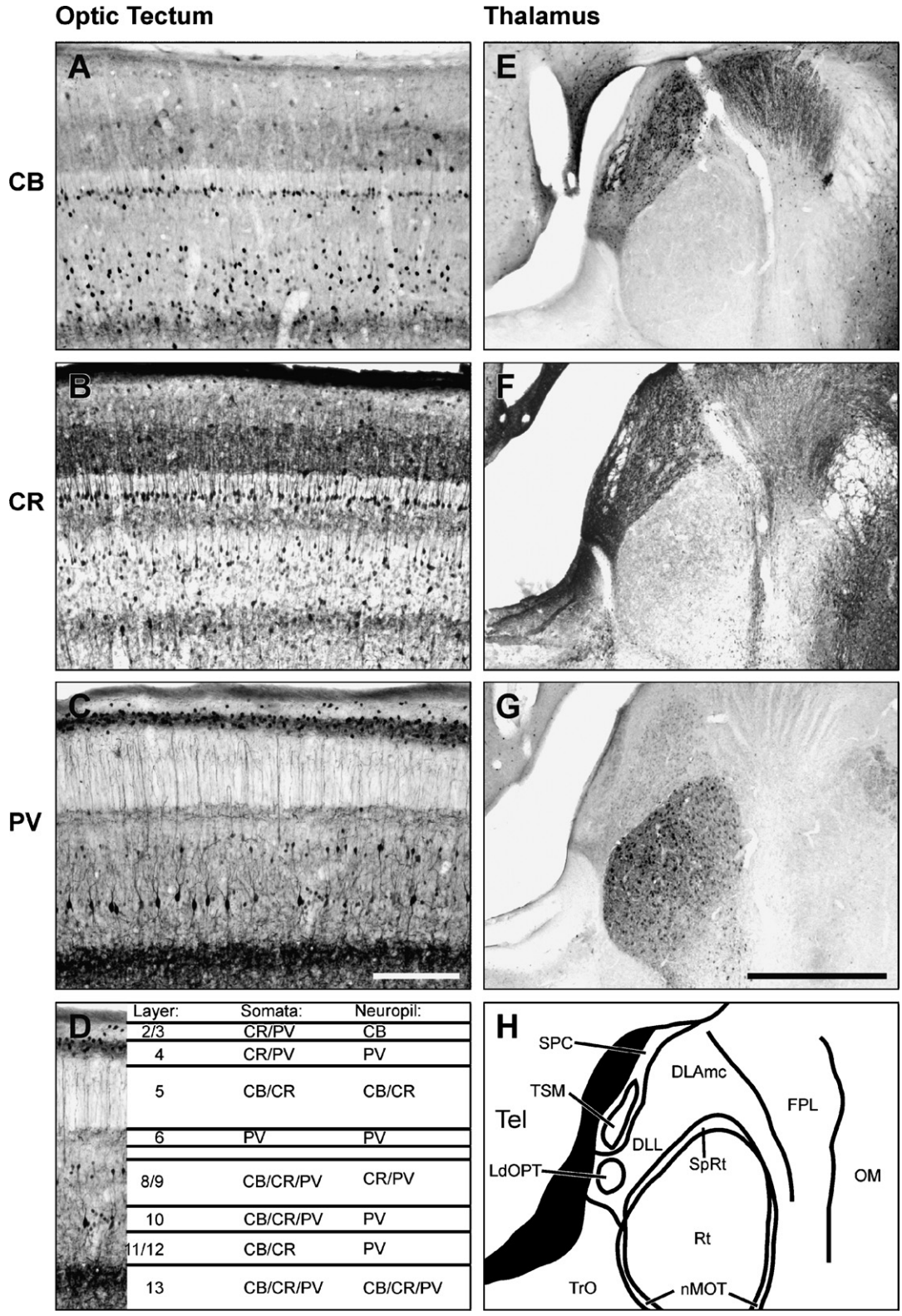

Fig. 2. Expression of calbindin (CB), calretinin (CR) and parvalbumin (PV) in frontal sections of the optic tectum (A–D) and the thalamus (E–H) of the zebra finch. (A–D) CB-ir neurons are found in layers 2–4, 5, 8 and 10–13, CB-ir fibers span layers 3, 5 and 13. CR-ir neurons are located in layers 2–5, 8 and 10–13 with dendrites covering layers 4, 5, 8 and 13. PV-ir neurons are found in layers 2–4, 6, 8–10 and 13 with fibers spanning tectal layers basal to layer 6, except for layer 7. Radial processes extend into superficial layer 4. Scale bar in C (for A–D): 200 μm. (E–H): In the lateral geniculate complex, CB-ir is found in DLA, DLL, LdOPT, SpRt and nMOT. CR-ir neurons and fibers have a comparable distribution as CB. PV-ir is completely absent in the Gld. The Rt completely lacks CB-immunoreactive neurons and dendrites. Few fibers within the Rt exhibit immunoreactivity against CR. Strong labeling against PV is observed in neurons within the Rt with a ventrally decreasing gradient. Scale bar in G (for E–H): 750 μm.

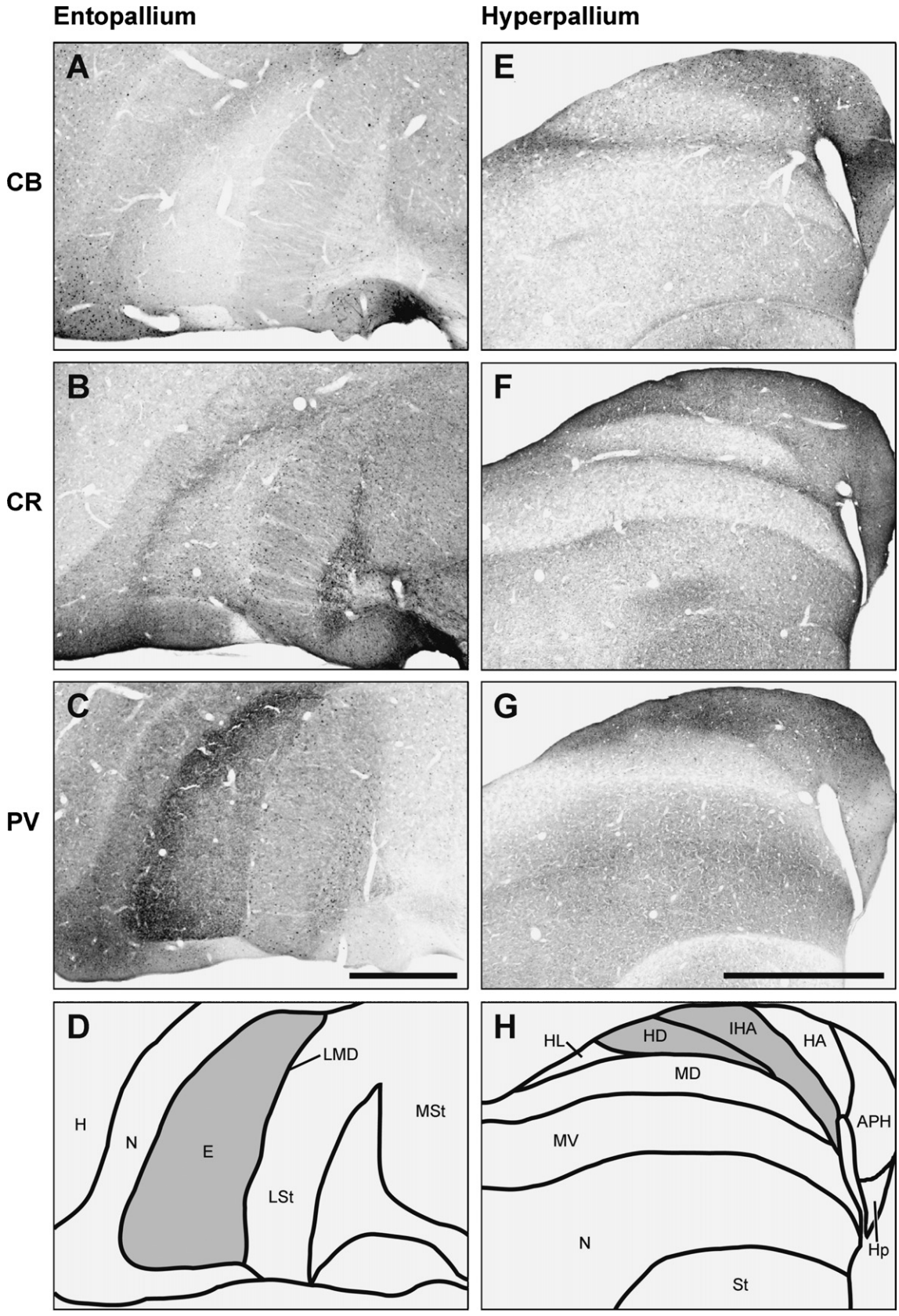

Fig. 3. Expression of calbindin (CB), calretinin (CR) and parvalbumin (PV) in frontal sections of the entopallium (A–D) and the hyperpalium (E–H) of the zebra finch. (A–C) CB-ir is completely absent. CR-ir are found in lateral portions. Immunoreactivity against PV is observed in the whole entopallium with an ascending gradient towards lateral portions. Scale bar in C (for A–D): 750 μm. (D): Respective immunosignals in tectal layers. (E–H): CB-ir neurons cover all wulst compartments. Additional fiber labeling is found in HA, IHA and HL. CR expression is observed in HA, IHA, HD and HL with intense fiber labeling in HD and HL subdivisions. PV-ir is found in HD, HL and IHA. Scale bar in G (for E–H): 1.5 mm.

4. Discussion

In this study, we show that three CaBPs characterize neuronal subpopulations in the zebra finch visual system. More specifically, certain CaBPs are differentially expressed in brain subdivisions generally corresponding to functional subpathways of the avian visual system. For example, the thalamofugal pathway is clearly delineated by a dominating expression of CB. In this pathway, retinofugal fibers curve into the contralateral GLd located in the dorsolateral thalamus [12], which strongly expresses CB (Fig. 2E and H). From here, bilateral projections lead to the visual wulst of the anteriodorsal forebrain [12,18]. The retinorecipient subdivisions of the visual wulst, especially the IHA, again are characterized by CB-immunoreactivity (Fig. 3E and H).

In contrast, PV-immunoreactive neurons are mainly found in parts of the tectofugal pathway, where retinofugal fibers arborize in layers 2–5 and 7 of the contralateral optic tectum [2,20,29]. In the zebra finch, PV is extensively expressed in retinorecipient layers of the optic tectum (Fig. 2C and D). Information is sent bilaterally to the thalamic Rt [5,25,22,30]. The Rt itself sends efferents to the ipsilateral telencephalic entopallium. Rt subregions as well as specific afferent target substructures in the entopallium [19,26] are characterized by strong immunoreactivity for PV (Fig. 2G and H; Fig. 3C and D). Apparently, PV labels neuronal subpopulations within all relay units of the tectofugal pathway, starting from deep tectal layer 13 via rostral parts of the Rt up to lateral entopallial portions. These findings give evidence for the theory of a topographic, functionally segregated arrangement of neurons in the tectofugal pathway, as suggested by various authors [16,30,34].

However, the general assumption that CaBPs might be completely segregated between the two visual pathways or even functional subpathways, as shown for the tectorotundal projection, cannot be upheld in the light of the labeling pattern for CR. Even though CR has a unique expression pattern that differs from both CB and PV, it is found in brain components of both visual pathways. Nevertheless, while it is still possible that CR marks a functional subsystem that is unknown so far, the differential expression between the tecto- and thalamofugal visual pathway is restricted to CB and PV.

In conclusion, our findings suggest that certain CaBPs not only identify morphological or neurochemical characteristics of individual neurons, but that they also associate with specific functional streams within brain components linked to vision in the zebra finch brain. This association with specific functional streams seems to be found in all participating brain structures, and apparently can be even applied to neuronal subsystems within one functional visual stream (as discussed above for e.g. a subpopulation of PV-positive neurons at all levels of the tectofugal pathway).

4.1. Comparison with other bird species

The specific expression pattern of CaBPs in the zebra finch brain is not identical to the patterns found in visual brain substructures of other bird species [33,39,45, H. Luksch, personal communication]. For example, in the pigeon, PV-expression in dendritic processes of the optic tectum spans all layers from layer 6 towards deep, efferent layers [33], whereas in the zebrafinch clear differences between single layers can be observed (e.g. absence of PV-positive neurons in layer 7). In the chicken optic tectum, far fewer neurons are labeled with antibodies against CR and PV than in corresponding brain structures of the zebra finch. Labeling against CB in layer 13 of the optic tectum in zebra finches is comparable to the one found in pigeons [33], whereas the chicken optic tectum completely lacks CB-immunoreactivity in this layer.

CB-immunoreactivity in the Rt stemming from tectorotundal projecting neurons found in pigeons [33] is completely absent in zebra finches. This suggests the existence of inter-bird-specific differences within functional tectal circuits. Since the expression of CaBPs is linked to the modulation of neuronal signals, each CaBP may label neuronal subpopulations exerting specialized functional features.

A previously published study provided a detailed analysis of CB expression in hyperpallial compartments of the chicken [45]. Here, CB-immunoreactive neurons showed a similar distribution as GABA. The present study in the zebra finch corroborate the findings of a differential expression of CB in the hyperpallium, which suggests that CB labels a subpopulation of GABAergic interneurons. In contrast, CR was found to label far fewer neurons in comparable hyperpallial compartments of the chicken [45] compared to the zebra finch. This, again, suggests that CR may label a subpopulation of GABAergic interneurons with little or no overlap with the CB-immunoreactive interneurons. Since similar distribution patterns were shown to exist in other pallial compartments of the bird brain e.g. [49] this seems to be a general feature of the avian nervous system.

In the pigeon entopallium, PV expression is stronger in central parts, whereas in the zebra finch, strongest PV expression is found in lateral portions (Fig. 3C and D). In principle, it is possible that these species differences are due to different antigen/antibody interactions or other experimental conditions. Since, however, avian brains are known to differ between avian orders, we believe that neural inter-species differences indicate a functional diversification at the level of single neuronal subsystems. Therefore, our findings cannot be easily generalized to all bird species.

4.2. Comparison with the mammalian visual system

CaBPs have been widely used to label specific cell groups in mammalian visual brain structures. Strikingly, the differential expression patterns of CB and PV are maintained at all levels of the mammalian visual system: a complementary distribution in the retina is maintained in the thalamus, accessory nuclei and the superior colliculus and, finally, can be found in the primary visual cortex [6,10,11,21,37,38,47]. Both proteins show a complementary laminar and columnar stratification corresponding to functional streams [9,46]: CB mainly labels the extrageniculocortical stream, PV is found in the geniculocortical stream [1,32].

Brain components belonging to the thalamofugal pathway in birds, which is suggested to correspond to the mammalian geniculostriate system [42], were shown to exhibit a preferential immunoreactivity against CB in zebra finches. In contrast, the avian tectofugal pathway, which is suggested to correspond to the mammalian extrageniculocortical visual stream, is dominated by immunoreactivity against PV in zebra finches. Thus, our data for expression of CaBPs in the zebra finch brain suggest that both mammals and birds show an almost complementary expression of CB and PV in visual substructures. However, the expression of CB and PV seems to be associated with opposite visual streams in mammals and birds.

4.3. Evolutionary aspects

The majority of studies on the expression patterns of CaBPs in visual brain components have been performed in mammals [1]. Our study assessed the expression patterns of CaBPs in zebra finches focussing on whether CaBP protein expression coincides with functional subcircuits within the songbird visual system. On the basis of our data, we report parallel findings in birds to the strikingly complementary distribution of CaBP in functionally connected visual brain structures of mammals. Thus, the contributions of the tectofugal and the thalamofugal pathway to separate aspects of visual processing appear to be comparable among vertebrate classes [7].

The finding that functionally connected brain structures express the same CaBP, has also been reported in parts of other sensory systems, such as the auditory system in songbirds [49]. These findings suggest that there might be a general evolutionary preference for a complementary expression of CaBPs, as this has now been shown for several sensory systems and vertebrate classes [15,26,49]. It is therefore tempting to speculate that CaBPs might help identify neuronal sub-circuits dedicated to specific functions.

Acknowledgements

Generous support was provided by the VolkswagenStiftung (grant on the program “dynamics and adaptivity of neuronal systems” to D.H., “Nachwuchsgruppe/Lichtenberg” grant to H.M.) and the Deutsche Forschungsgemeinschaft (FOR 701 and MO 1408/1-2 grants to H.M.; Lu 622/8 grant to H.L.; SFB 509 to M.M. and O.G.). The authors thank members of their groups for technical expertise in the lab and constructive criticism on the manuscript.

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