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ORGANIZATION OF TELENCEPHALOTECTAL PROJECTIONS IN PIGEONS: IMPACT FOR LATERALIZED TOP-DOWN CONTROL

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Abstract—Birds display hemispheric specific modes of visual processing with a dominance of the right eye/left hemisphere for detailed visual object analysis. In pigeons, this behavioral lateralization is accompanied by morphological left–right differences in the ascending tectofugal pathway. This system is also asymmetrically modulated by descending telencephalotectal input whereby the left forebrain displays a much more pronounced physiological control over ipsilateral left and contralateral right visual thalamic processes. In the present study we aimed to answer the question if this top-down asymmetry that up to now had been demonstrated in single cell recording studies is due to anatomical asymmetries in the size of the fiber systems descending from the telencephalon to the tectum.

We approached this question by means of a quantitative retrograde tracing study. Cholera toxin subunit B (CtB) was injected unilaterally into either the left or right optic tectum of adult pigeons. After immunohistochemical detection of CtB-positive cells, the number of ipsi- and contralaterally projecting neurons was estimated. Retrogradely labeled cells were located within the arcopallium, the hyperpallium apicale (HA) and the temporo-parieto-occipital area (TPO). Descending projections from HA, arcopallium, and TPO were mainly or exclusively ipsilateral with the contralateral projection being extremely small. Moreover, there was no difference between left and right hemispheric projections. These anatomical data sharply contrast with behavioral and electrophysiological ones which reveal an asymmetric and bilateral top down control. Therefore, contralateral and lateralized forebrain influences onto tectofugal processing are possibly not the direct result of asymmetrical descending axon numbers. Those influences emerge by a lateralized intra- and/or interhemispheric integration of ascending and descending input onto the rotundus.

Key words: arcopallium, birds, cholera toxin subunit B, tectofugal, tract tracing, visual Wulst.

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Abbreviations: AA, arcopallium anterior; AD, arcopallium dorsale; AI, arcopallium intermedium; AM, arcopallium mediale; CDL, dorsolateral corticoid area/area corticoidea dorsolateralis; CtB, cholera toxin subunit B; GLd, nucleus geniculatus lateralis dorsalis; HA, hyperpallium apicale; Ipc, nucleus isthmi parvocellularis; NFL, frontolateral nidopallium; NI, intermediate nidopallium; PBS, phosphate-buffered saline; PBS+, 0.12 M phosphate-buffered saline+0.3% Triton X-100; PoA, nucleus posterioris amygdalopalli; PT, nucleus pretectalis; Slu, nucleus isthmi semilunaris; TOM, tractus occipitomesencephalicus; TPO, temporo-parieto-occipital area; TSM, tractus septomesencephalicus; VLT, nucleus ventrolateralis thalami.

An increasing amount of evidence demonstrates differences between left- and right-hemispheric processing in all vertebrates (Vallortigara et al., 1999; Rogers and Andrew, 2002; Vallortigara and Rogers, 2005). Especially the visual system has been extensively analyzed, since the virtually complete crossing of the optic nerves in all non-mammalian species enables behavioral paradigms with sight restricted to one eye and thus the contralateral hemisphere. Studies in birds have shown that the left hemisphere is specialized for detailed visual object analysis (Mench and Andrew, 1986; Güntürkün and Kesch, 1987; Vallortigara and Andrew, 1994; Rogers, 1997; Valenti et al., 2003), while the right hemisphere extracts relational configurations of visual stimuli (Clayton and Krebs, 1994; Kahn and Bingman, 2004; Tommasi and Vallortigara, 2001, 2004; Vallortigara et al., 2004) and responds to novelty and reactivity to predators (Rogers, 2002). These hemispheric-specific processing modes might be related to differential electrophysiological characteristics of single units within the ascending information processing stream (Folta et al., 2004).

Functional lateralization is accompanied by anatomical asymmetries within the ascending visual tecto- and thalamofugal pathways. In chicks, pharmacological (Deng and Rogers, 2002) and anatomical studies show the thalamofugal system to be asymmetrically organized (Rogers and Deng, 1999; Koshiba et al., 2003). This pathway transfers visual information via the dorsolateral geniculate complex (nucleus geniculatus lateralis dorsalis, GLd) onto the telencephalic visual Wulst whereby the left GLd gives rise to more bilateral projections onto the Wulst than the right one. In contrast, the tectofugal system is characterized by left–right differences in pigeons. This pathway conveys visual input via the optic tectum and nucleus rotundus onto the forebrain. Apart from cell size asymmetries at tectal (Güntürkün, 1997; Skiba et al., 2002; Manns and Güntürkün, 1999a, 2003) and rotundal (Manns and Güntürkün, 1999b) level, the tectorotundal projection is asymmetrically organized with more fibers crossing from the right tectum to the left rotundus than vice versa, enabling a more bilateral representation within the left rotundus (Güntürkün et al., 1998).

While these studies demonstrated asymmetries within the ascending visual pathways, recent research also evinced the presence of asymmetric top-down forebrain control onto tectofugal processing. Folta et al. (2004) revealed that single cells of the rotundus integrate ascending and descending information in a lateralized way. Especially very late responses that probably derived entirely from the forebrain originated exclusively from the left hemi-

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sphere. This pattern was observed for single neurons within the left and the right rotundus. This result would suggest that executive control over left and right thalamic visual analysis is modulated by the left hemisphere only. Valencia-Alfonso et al. (2005) in addition could show that the left Wulst modulates visual responses of single rotundal neurons in the left and the right thalamus in a more pronounced way than the right Wulst.

Telencephalic efferents onto the diencephalon and the brainstem arise from two major descending pathways, the tractus occipitomesencephalicus (TOM) and the tractus septomesencephalicus (TSM). None of them directly contacts rotundal neurons, but both terminate massively onto the optic tectum from where projections ascend to the rotundus. The neurons which constitute the TOM are located within the arcopallium (nomenclature according to Reiner et al., 2004) and send projections mainly onto tectal layers 13 and 14 (Zeier and Karten, 1971, 1973; Dubbeldam et al., 1997). The neurons constituting the TSM are located within the Wulst and terminate predominantly within efferent lamina 13 but also within the superficial layers 2–4, 6, 7 and 12 (Leresche et al., 1983; Reiner and Karten, 1983; Miceli et al., 1987). Folta et al. (2004) and Valencia-Alfonso et al. (2005) could pharmacologically ascertain that the Wulst participates in the lateralized top-down modulation. Presently it is unclear if the arcopallium is also involved via the TOM in the constitution of left–right-differences of top-down control.

Comparable to the bottom-up projections, it is therefore conceivable that the telencephalotectal projection pattern displays structural left–right differences. According to Folta et al. (2004) and Valencia-Alfonso et al. (2005) we would expect bilateral projections arising from the left Wulst onto the tectum. However, studies of Karten et al. (1973) and Miceli and Repérant (1983) described only an extremely limited amount of contralateral projections in pigeons. In contrast, Bagnoli et al. (1980) reported a high number of Wulst cells descending to the contralateral tectum. In order to clarify the functional architecture of the telencephalotectal system, we performed tectal tracer injections to investigate qualitative and/or quantitative left–right differences.

EXPERIMENTAL PROCEDURES

Twenty-two adult pigeons (*Columba livia*) of unknown sex from local breeding stocks were used in this study whereby 11 animals received cholera toxin subunit B (CtB; Sigma, Munich, Germany) injections into the left and 11 into the right tectum. All experiments were carried out according to the specifications of the German law for the prevention of cruelty to animals and hence, the European Communities Council Directive of 24 November 1986. All efforts were made to minimize the number of animals used and their suffering.

Prior to surgery, the pigeons were anesthetized with equithesin (0.3 ml per 100 g body weight) and were placed into a stereotaxic apparatus (Karten and Hodos, 1967). For tectal tracer injections, a modified device was used which allowed lateral rotation of the head along the longitudinal axis over 100° to the left and right (Hellmann and Güntürkün, 1999). The scalps were infiltrated with Xylocaine and incised between the eye and ear holes and the skull was opened with a dental drill. A glass micropipette (outer tip diameter 15–20 μm) mounted to a mechanic pressure device (WPI Nanoliterinjector; World Precision Instruments, Berlin, Germany) was inserted into tectal layers according to stereotaxic coordinates of the pigeon brain atlas by Karten and Hodos (1967). Injections were performed in three steps with injection depths ranging from 0.7–1.5 mm. At each depth about 100 nl CtB was applied.

After 2 days' survival time, animals received an injection of 200 units sodium heparin and were then deeply anesthetized with an overdose of equithesin (0.5 ml per 100 g body weight). The pigeons were perfused through the heart with 200 ml 0.9% sodium chloride and 800 ml ice-cold 4% paraformaldehyde in 0.12 M phosphate-buffered saline (PBS), pH 7.4. The brains were removed and postfixed for 2 h in fixative with supplement of 30% sucrose. Subsequently, the brains were cryoprotected overnight in a solution of 30% sucrose in 0.12 M PBS. The brains were cut in frontal plane at 40 μm on a freezing microtome and the slices were collected in PBS containing 0.1% sodium azide.

Brain slices were reacted free-floating according to the immuno-ABC-technique (Hellmann and Güntürkün, 2001). The sections were placed for 30 min in 0.3% hydrogen peroxide in distilled water to reduce endogenous peroxidase activity. After blocking unspecific binding sites with 10% normal goat serum for one hour, sections were incubated overnight at 4 °C in the primary antibody solution (rabbit anti-choleragenoid; Sigma; 1/10,000 in 0.12 M phosphate-buffered saline+0.3% Triton X-100 (PBS+)). After being rinsed, the sections were incubated for 60 min at room temperature in the biotinylated secondary antibody solution (goat anti-rabbit; Vectastain, Vector, Camon (Wiesbaden, Germany); 1/250 in PBS+). After additional rinsing, the sections were incubated for 60 min in avidin–biotin–peroxidase solution (Vectastain ABC-Elite kit, Vector, Camon; 1/100 in PBS+). After washing, the peroxidase-activity was detected using a heavy metal intensified 3′3-diaminobenzidine (DAB; Sigma) reaction, modified by the use of b-[d[r]-glucose/glucose-oxidase (Sigma; Hellmann and Güntürkün, 2001). The sections were mounted on gelatin-coated slides, dehydrated and coverslipped with Permount (Fisher Scientific, Hampton, NH, USA).

The number of ipsi- and contralaterally labeled cells within hyperpallium apicale (HA), temporo-parieto-occipital area (TPO), and arcopallium (nomenclature according to Reiner et al., 2004) was estimated along the complete rostro-caudal extent of the forebrain hemispheres by counting CtB-positive cells in every 10th section with 450× magnification at a Leica DML microscope (Leica Microsystems, Wetzlar, Germany). Quotient of counted cells and analyzed sections was used as a measure for cell number in each preparation. Since the absolute number of labeled cells depends on the applied tracer amount, the injection volume was estimated (Fig. 1). Gray tone pictures were converted into binary black and white ones and the size of black areas was estimated with the image analyzing system analySIS 2.0 (SIS; Münster, Germany) a Olympus BH2 microscope (Olympus, Tokyo, Japan) with 4×1.25×1.6 magnification. Injection volume was calculated as the summed area of the serial outlines multiplied by the section thickness. For quantitative analysis, we divided cell number by injection volume to correct cell number for injection size. Moreover, we estimated the area of forebrain structures with labeled neurons with the image analyzing system analySIS 3.0 (SIS) to calculate analyzed volume and density of labeled cells. Statistical analysis was performed with the statistic program Statistica (StatSoft, Tulsa, OK, USA). Photographic documentation was carried out using a digital camera-system (Zeiss Axiocam; Zeiss, Jena, Germany) attached to the microscope. Images were processed with Zeiss Axiovision 3.0 and color balance, contrast, and brightness were adjusted with Photoshop 5.5 software (Adobe, Germany).

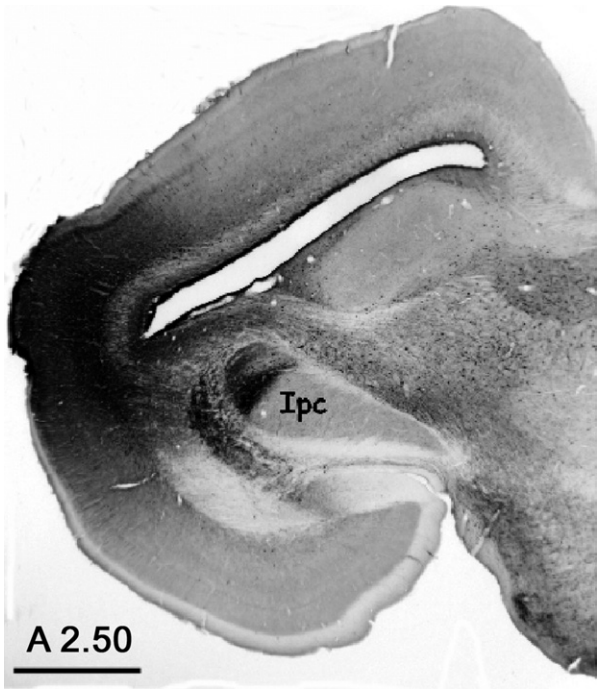

Fig. 1. Tracer application site with the injection being placed within the lateral tectum; note labeling of the dorsal portion of the Ipc. Scale bar=1000 μm.

RESULTS

Tectal tracer application gave rise to retrograde labeling of cell populations in several structures. Telencephalic afferents were located within the HA, most substructures of the arcopallium, and the area TPO.

Arcopallial labeling extended between A 5.25 and A 7.25 and included cells located within AD (arcopallium dorsale), AI (arcopallium intermedium) and in most cases AM (arcopallium mediale; Fig. 2a). No labeling could be detected within AA (arcopallium anterior). On average 406 cells/section were labeled, with the traced neurons being clustered in high density (255 cells/mm^2). Cells displayed a multipolar shape and were separated by a dense dendritic arborization network (Fig. 2c). On average, just 15 contralateral cells could be identified, hence the contralaterally projecting population was very small and encompassed about 2% of the labeled arcopallial neurons (Fig. 2b). In most cases, no contralaterally located cells could be detected at all while one case displayed 94 labeled neurons.

CtB-labeled cells within HA were mostly located between A 7.0 and A 14.00. In mean, 113 cells/section could be counted. Compared with the arcopallium, cell densities were much smaller and only reached 56 cells/mm^2 (Fig. 3a). Labeled neurons consisted of two cell types. Most neurons displayed a multipolar shape but a minority had small fusiform or triangular cell bodies (Fig. 3c). The number of contralaterally located cells varied between 0 and 35 cells with a mean of six cells, hence representing only 0.5% of all labeled neurons (Fig. 3b).

Separated by a small gap from neurons located in HA, another multipolar cell population could be observed along the dorsolateral surface which was completely confined to the ipsilateral hemisphere (Fig. 4a, b). These cells were located between rostrocaudal levels A 6.75 and A 9.00. In mean, 45 cells/section could be detected and the density of labeled cells was comparable to HA with 54 cells/mm^2. According to the Karten and Hodos (1967) atlas, the rostrocaudal positions of labeled cells included area corticoidea dorsolateralis (CDL) as well as area TPO. However, by means of tract tracer applications, a recent study by Atoji et al. (2005) could show that caudally located cells give rise to reciprocal connections with limbic structures, while rostrally located cells have more connections with the striatum and visual structures. The authors suggest that the approximate level of transition between CDL and TPO corresponds to level A 6.50. Therefore, we classified cells projecting to the tectum as located within TPO. In our preparations, these cells were virtually confined to the dorsal aspect of TPO although the TPO expands more laterally (Fig. 4a). Since our tracer injections were confined to the lateral tectum, this restricted labeling pattern might indicate a topographical projection.

Quantitative differences between left and right tectal injections

For a quantitative analysis of left and right hemispheric telencephalotectal projections, care was taken to make sure that application sites did not vary to ensure homogeneity of the labeling pattern. To this end, tracer injections were placed approximately at the same rostrocaudal and dorsoventral levels since the telencephalotectal projection is known to be topographically organized (Miceli et al., 1987). We confined a consistent application to the mediolateral tectum (Fig. 1) by controlling the location of labeling in four topographically organized projections to and from the tectum:

i) a column-like staining of the dorsal Ipc (nucleus isthmi parvocellularis; Fig. 1; Güntürkün and Remy, 1990; Wang et al., 2006),
ii) retrogradely labeled neurons within the dorsal cap of the Slu (nucleus isthmi semilunaris; Hellmann et al., 2001),
iii) a dense spot of anterogradely labeled fibers spanning through the dorsoventral axis of the medial GLv (nucleus geniculatus ventralis; Crossland and Uchwat, 1979),
iv) and a focus of labeled fibers at the ventrolateral aspect of the ION (nucleus isthmo-opticus; Crossland and Hughes, 1978).

In addition, we checked that all tracer injections included all tectal layers receiving ipsi- and/or contralateral forebrain input. Arcopallial cells terminate within the deep tectal layers (Zeier and Karten, 1971; Dubbeldam et al., 1997) while afferents from the Wulst terminate within layers 2–4, 6, 7, 12, and 13 (Miceli et al., 1987). Injections into all these target layers could be verified by labeling of other efferent and afferent tectal connections.

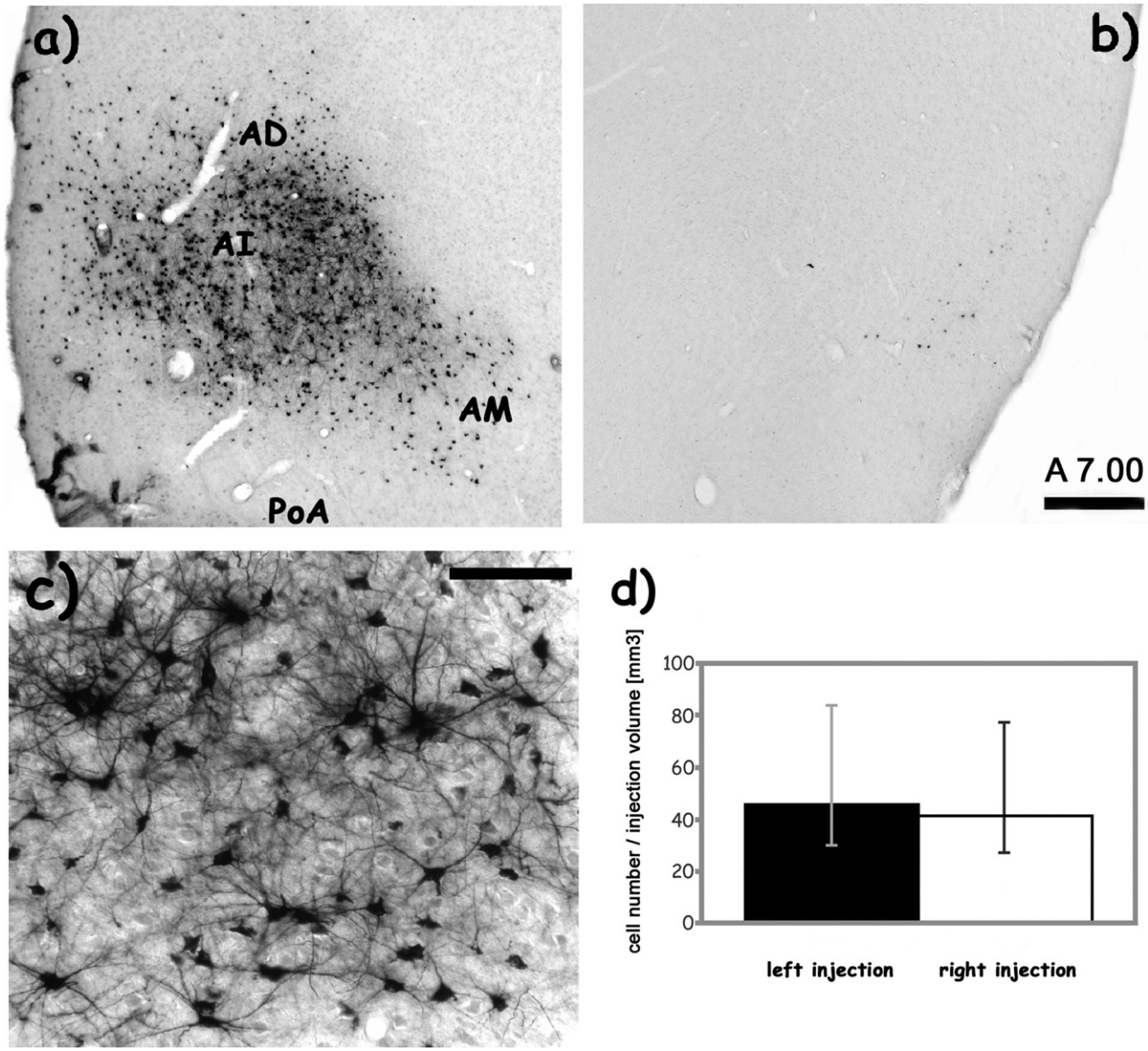

Fig. 2. Labeling within the arcopallium. Retrogradely labeled neurons located within the ipsilateral AD, AI, AM (a). Just a small number of cells could be identified within the contralateral AI (b). A dense network of multipolar neurons was detected within the ipsilateral AI (c). The relative cell number expressed as the median number of labeled cells/mm^3 injection volume did not differ after left and right tectal injections (d). Scale bar=1000 μm in a–b and 100 μm in c, and 25%–75% quartiles in d.

i) Tracer application within layer 13 was confirmed by bilateral fiber staining within the nucleus rotundus (Hellmann and Güntürkün, 1999), within the mainly contralaterally descending tectobulbar as well as the mainly ipsilaterally projecting tectopetal fiber tracts (Hellmann et al., 2004).

ii) Tracer application into the superficial laminae was confirmed by labeled cells located within Ipc which projects onto layers 2–13 (Wang et al., 2006), Imc (nucleus isthmi magnocellularis) which terminates in layers 10–12 (Wang et al., 2004), Slu which project onto the layers 4–13 (Hellmann et al., 2001; Wang et al., 2006), PT (nucleus pretectalis) which projects onto layer 5 (Gamlin et al., 1996), and VLT (nucleus ventrolateralis thalami) which projects onto layers 11–14 (Hunt and Brecha, 1984; Schulte et al., 2006).

iii) Moreover, bilateral cellular labeling of PT, LLd (nucleus lemnisci lateralis, pars dorsalis) and VLT verified labeling of ipsi- as well as contralaterally located cell populations.

Only injections that fulfilled these criteria were taken into account.

Application volumes varied between 12 mm^3 and 60 mm^3 and there was no significant difference between left- and right-sided injections (Mann-Whitney U: $Z=0.756$; $P=0.450$). In four cases, tracer spread into the ventricle, resulting in a complete staining of the ventricular epithe-

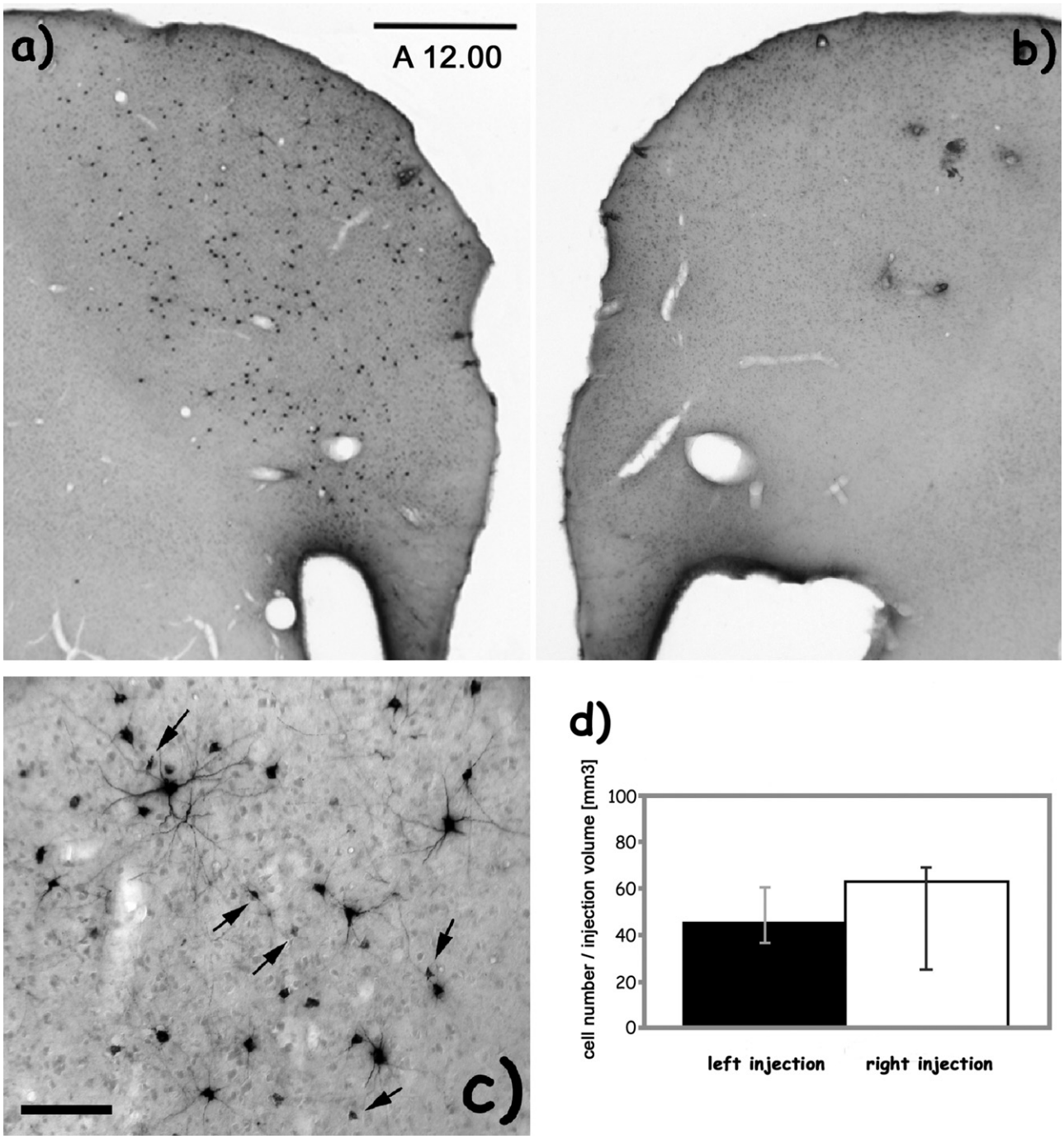

Fig. 3. Labeling within HA-retrogradely labeled neurons located within the ipsilateral HA (a). Virtually no cells could be identified within the contralateral hemisphere (b). The telencephalotectally projecting cell population consisted of at least two cell classes (c): Apart from large multipolar neurons, smaller more fusiform cells could also be detected (arrows). There was no difference in the relative cell number after left- and right-tectal injections (d). Scale bar=1000 μm in a–b and 100 μm in c, and 25%–75% quartiles in d.

lium and in a bilateral labeling of all medial cell populations within the hypothalamus, the hippocampus and the Wulst. We excluded these cases. Due to their negligible number, contralateral cells were not included into the quantitative analysis. Due to large variation in relative cell number which did not display a normal distribution, we calculated the median of left and right tectal injections as a measure of central tendency to illustrate left–right differences in projection pattern.

Comparing the overall number of telencephalotectal cells, there was no difference in the amount of left- and right-hemispheric projections with 128 cells/mm^3 tectal injection volume within the right and 109 cells/mm^3 tectal injection volume within the left hemisphere (Mann-Whitney

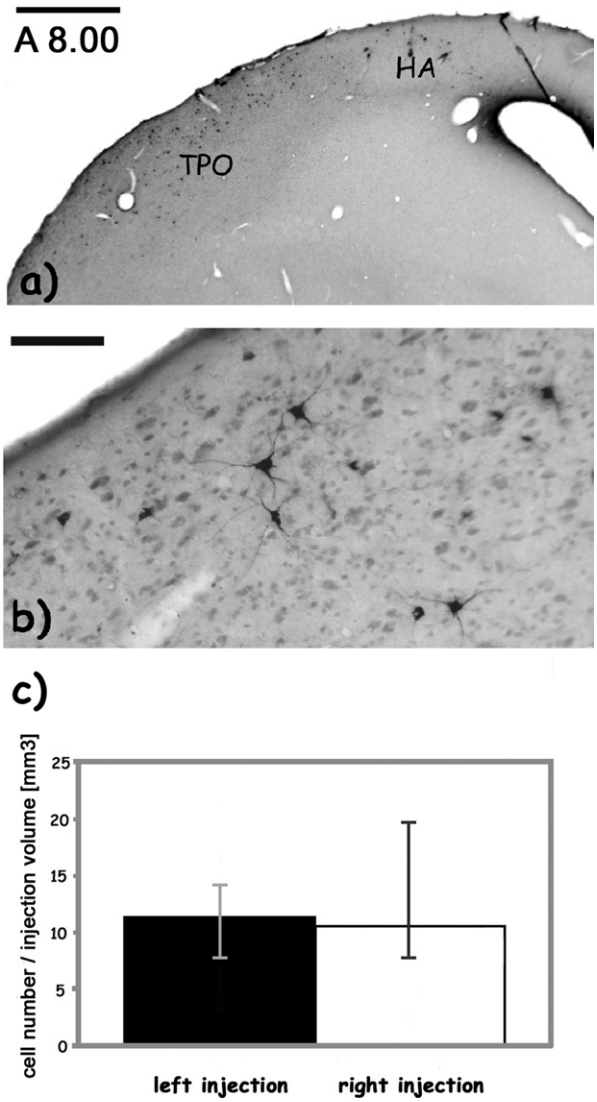

Fig. 4. Labeling within TPO. Retrogradely labeled neurons were confined to the ipsilateral hemisphere. This cell population was separated by a small gap from labeled neurons located in HA (a). The telencephalotectally projecting cell population consisted of multipolar neurons of different size (b). There was no difference in the relative cell number after left- and right-tectal injections (d). Scale bar=1000 μm in a and 100 μm in b, and 25%–75% quartiles in d.

U: Z=−0.163; *P*=0.870). Specific analyses of the arcopallium evinced a median number of 47 cells/mm^3 tectal injection volume after left and a median number of 55 cells/mm^3 tectal injection volume after right tectal injections (Mann-Whitney *U*: Z=0.163; *P*=0.870; Fig. 2d). HA displayed a median number of 45 cells/mm^3 tectal injection volume after left- and 62 cells/mm^3 tectal injection volume after right-tectal injections (Mann-Whitney *U*: Z=−0.572; *P*=0.568; Fig. 3d). Within TPO, a median number of 11 or 10 cells/mm^3 tectal injection volume could be determined after left- or right-tectal injections, respectively (Mann-Whitney *U*: Z=−0.089; *P*=0.929; Fig. 4c).

The absence of significant differences in the number of counted cells did not result from differences in the volume size of analyzed areas, neither within the arcopallium (left-tectal injection: 8.0 mm^3; right-tectal injection: 7.7 mm^3; Mann-Whitney *U*: Z=0.751; *P*=0.453) nor HA (left-tectal injection: 122.5 mm^3; right-tectal injection: 117.8 mm^3 Mann-Whitney *U*: Z=1.103; *P*=0.270), or TPO (left-tectal injection: 20.4 mm^2; right-tectal injection: 11.5 mm^3; Mann-Whitney *U*: Z=1.634; *P*=0.102).

DISCUSSION

The present study examined the quantitative organization of telencephalotectal projections in pigeons. Our results revealed that telencephalotectal projections are mostly ipsilaterally organized and that the left and right hemispheres contribute equally to these connections. Thus, asymmetric top-down control onto rotundal processing (Folta et al., 2004; Valencia-Alfonso et al., 2005) emerges probably only by lateralized intra- and/or intertectal integration of bottom-up and top-down projections.

Telencephalotectal projection pattern

CtB-injections evinced a virtually complete “ipsilaterality” of telencephalotectal projections. While no contralateral fibers have been reported arising from the arcopallium (Zeier and Karten, 1971; Davies et al., 1997; Dubbeldam et al., 1997) or TPO (Atoji and Wild, 2005) the projection pattern of hyperpallial efferents is controversially discussed in the literature. In contrast to the studies of Karten et al. (1973) or Miceli and Repérant (1983), Bagnoli et al. (1980) reported a high number of Wulst cells descending to the contralateral tectum after horseradish-peroxidase (HRP) injections in pigeons. The absence of contralateral projections was confirmed in the present study, which was performed with the most sensitive retrograde tracer available (Kobbert et al., 2000). Extensive bilateral labeling was only observed in cases where the ventricular epithelium was stained and thus, tracer spread into the ventricles had occurred. Such tracer spread may provide an explanation for the high number of bilateral projections in the study of Bagnoli et al. (1980).

Based on various anatomical evidence, the former archistriatum of the avian forebrain has been subdivided into a somatomotor arcopallium and a limbic amygdala (Reiner et al., 2004). Each of these two entities is constituted by various further subdivisions. The avian amygdala seems to be composed by the posterior pallial amygdala (PoA), the subpallial amygdala (SpA) and the n. taeniae of the pallial amygdala (TnA). We did not detect any labeled neurons located in any of these structures after tectal CtB-injections. The somatomotor arcopallium, which is assumed to be involved in sensorimotor control e.g. for vocalization (Wild et al., 1993) or feeding behavior (Zeier, 1971; Dubbeldam and Den Boer-Visser, 1994), has been subdivided into AA, AD, AI and AM. But it is unclear if AA represents a distinct entity or a continuation of AI (Reiner et al., 2004). In our preparations, telencephalotectal cells are located in AD, AI and AM but not in AA. This pattern suggests AA as a truly discrete arcopallial subdivision separated from AI.

The main projections descending within the TSM arise from HA (Reiner and Karten, 1983). HA represents that part of the visual Wulst which constitutes the source of intra- and extratelencephalic projections and which receives thalamofugal visual input via IHA (interstitial nucleus of HA), HD (hyperpallium densocellulare), and HI (hyperpallium intercalatum). In addition, HA receives intratelencephalic input from intermediate (NI) and frontolateral (NFL) nidopallium and somatic arcopallial input from AI (Shimizu et al., 1995; Deng and Rogers, 2000). It is unknown if these differential inputs contact distinct HA neurons which in turn give rise to distinct descending projections. The presence of separated efferent projections is supported by the fact that HA fibers terminate within different tectal laminae and by the detection of different efferent cell types. In our preparations, large, multipolar neurons could be distinguished from a minor population of smaller fusiform cells.

TPO resembles HA with respect to morphology and density of projection neurons but it is not clear if their descending fibers terminate in distinct tectal laminae and hence, if they are connected with different tectal neurons. TPO receives input from HA, and HL (hyperpallium laterale) as well as from the peri-entopallium (Ep2) (Husband and Shimizu, 1999; Atoji and Wild, 2005) indicating that TPO establishes a feedback loop between the tecto- and thalamofugal system. Moreover, intratelencephalic input comes from CDL, the NI lateral (NIL), NFL and caudolateral (NCL) nidopallium, as well as from the ventrolateral part of the basolateral layer of PoA, and hence from the amygdala (Atoji et al., 2005). This might suggest that TPO is embedded into a telencephalotectal side pathway integrating visceral aspects into visual analysis.

Interhemispheric interactions mediating asymmetric top-down control

At first glance, the symmetry and the ipsilaterality of the telencephalotectal projections contradict the recent physiological findings from rotundal single-unit recordings. These data have shown that it is primarily the left hemisphere where top-down control onto tectofugal processing takes place. Pharmacological studies demonstrated that the left visual Wulst impacts rotundal activity patterns on both sides to a significantly stronger degree than the right Wulst (Folta et al., 2004; Valencia-Alfonso et al., 2005). The most parsimonious explanation for these electrophysiological data would be the existence of anatomical differences in the bilaterally descending telencephalotectal system. This is exactly what we tested but could not reveal. Neither is the telencephalotectal system, with respect to the number of constituting cells, asymmetrically organized nor does it display a substantial contralateral projection. According to the present anatomical data, we have to conclude that the asymmetric top-down effects shown in single-cell recording studies do not directly arise from left–right differences in the amount of descending forebrain projections. However, this pattern does not exclude asymmetric synaptic transmission resulting from left–right differences in the amount of e.g. dendrites, synaptic contacts and/or neurotransmitter receptors.

To understand this seeming contradiction, one first has to state that the physiological top-down effects had been examined at rotundal level while TSM as well as TOM fibers terminate within the optic tectum. Therefore, telencephalic influences onto rotundal processing must be mediated by circuits passing through the tectum which in turn ascends bilaterally onto the rotundus. This projection is asymmetrically organized with more fibers ascending from the right tectum to the left rotundus than vice versa (Güntürkün et al., 1998). Accordingly, a stronger modulation of left rotundal processing might be a direct consequence of this stronger bilateral tectal input terminating on the left thalamic side. However, this network does not explain why the right rotundus system is less modulated by right forebrain input despite the presence of a prominent direct telencephalotecal projection. It is conceivable that this is the result of suppressive subtelencephalic interactions. In fact, the mainly inhibitory intertectal commissures (Robert and Cuénod, 1969; Hardy et al., 1984) are asymmetrically organized with a stronger influence of the left tectum onto the right one (Keysers et al., 2000). Transection of the tectotectal commissures leads to a reversal of the normal lateralization pattern (Güntürkün and Böhringer, 1987) indicating that the functional lateralization pattern depends on a dynamic balance between left and right tectal processing (Skiba et al., 2000). The importance of dynamic process-dependent principles is supported by studies which show that behavioral deficits provoked by unilateral lesions of descending forebrain systems differ profoundly from bilateral ones (Nau and Delius, 1981; Güntürkün and Hoferichter, 1985).

Moreover, apart from inhibitory interactions at tectal level, suppressive influences might directly affect rotundal neurons by GABAergic input from the bed nuclei of the tectothalamic tract. These nuclei receive a side branch of the tectorotundal projection from both half brains and from PT (Theiss et al., 2003) and are involved in the regulation of ipsilateral as well as bilateral visual input (Voss and Bischof, 2003). It has been assumed that this system is involved in the shift of the balance of the attentional resources between the two visual half fields (Theiss et al., 2003). A stronger activation within the right tectorotundal system might specifically suppress top-down influenced rotundal cells and hence, might be involved in the regulation of lateralized visual analysis. However, since this system is also activated by the optic tectum, in sum several lines of evidence suggest the tectum as a crucial station of visual information processing integrating ascending bottom-up and descending top-down information depending on the actual input from the left and right eye. As a result, it is likely the tectal but not the telencephalic level which is responsible for lateralized visual information flow in pigeons. Accordingly, the telencephalotectal projection system is not asymmetrically organized since the impact of top-down control might depend on the necessary mode of visual analysis.

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