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ALTHOUGH functional asymmetries in the course of visual information processing have been known for a long time in humans as well as in non-human species, the structural basis of these asymmetries is largely unknown. We now report that due to an asymmetry of commissural projections in the pigeon the left nucleus rotundus of the ascending tectofugal visual system predominantly represents inputs from both eyes while the right nucleus rotundus mainly represents the contralateral left eye. We suggest that a comparable organization exists for several asymmetries in humans. A representation of both hemifields can provide the dominant hemisphere with direct access to all stimulus features when objects cross the vertical meridian. *NeuroReport* 9: 4127–4130 © 1998 Lippincott Williams & Wilkins.

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Asymmetries of representation in the visual system of pigeons

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Introduction

In vertebrates, input from the visual hemifields is processed almost exclusively by the contralateral brain hemisphere during the first stages of processing. The integration of visual percepts from the two sides into a complete visual scene is enabled by commissural projections which connect the two brain hemispheres and thus the representations from the two visual hemifields. In humans and non-human vertebrates, particularly birds, a number of functional asymmetries on visual tasks has been reported.^{1,2} Due to the virtually complete decussation of the optic nerves in birds, visual lateralization can easily be studied by means of eyecaps which restrict primary visual input into one hemisphere during discrimination tasks. With this procedure chicks and pigeons were shown to reach significantly higher levels of performance with the right eye/left hemisphere in discriminating between grain and grit,^{1,3} between colors or artificial patterns^{4,5} or between 725 abstract patterns which had to be memorized.⁶ While spatial visual cues seem to be often processed with a superiority of the right hemisphere, behavioral tasks involving visual feature detection are primarily under left hemispheric control.¹

Experiments with unilateral lesions of the n. rotundus demonstrated that the tectofugal pathway is responsible for visual feature analysis.^{7,8} Within this ascending pathway to the forebrain, visual input is transferred via retinal ganglion cells to the contralateral tectum. Tectal layer 13 cells project onto

thalamic nucleus rotundus, from where output arises to the telencephalic ectostriatum.⁹ Although retinal input is nearly completely crossed and consequently unilateral, each hemisphere receives input from both eyes, realized by bilateral projections from tectum to rotundus.¹⁰

To test whether representational differences and functional asymmetries between the left and right brain hemisphere might be due to commissural asymmetries, we quantitatively examined the tectorotundal projections by means of retrograde and anterograde tract tracing techniques. We used the retrograde tracer rhodamine to determine the numbers of tectal cells projecting from the ipsi- and contralateral tectum to the left and right nucleus rotundus. Rhodamine was previously shown to excellently trace ipsilateral and contralateral tectorotundal projections.¹¹ Additionally, retrograde tracing data were quantitatively verified, using the anterograde tracer biotinylated dextran amine (BDA).

Materials and Methods

Rotundal tracer injections: Thirty-four adult pigeons received injections of 50 nl rhodamine into the core of nucleus rotundus (Rt) at coordinates A6.00, L3.00, D6.00¹² as described previously.¹¹ Only those 20 birds (10 left, 10 right) in which injection was completely inside Rt and in which no tectal cells outside lamina 13 were labeled were used for analysis. After 24–72 h survival time subjects were deeply anaesthetized and perfused with 4% paraformaldehyde.

hyde in 0.1 MPBS (pH 7.4). Brains were cryoprotected by immersion in 25% (w/v) sucrose solution in 0.12 M PBS for 6 h and 25 μ m sections were processed. Survival time was balanced between the two groups. Injection volume was calculated from serial sections with an image analysing system by measuring the brightly fluorescing injection zone.¹¹ In every second tectal section labeled neurons of the complete extent of layers 13 of left and right tectum were counted using an epifluorescence microscope with a $\times 20$ UVFL objective and an Olympus G filter block. Complete length extents of left and right layers 13 were normalized¹¹ to correct for possible misalignments during sectioning. Cell counts were corrected according to Floderus.¹³

Tectal tracer injections: BDA (110 nl, 10%; 10 000 mol. wt, lysine fixable) was pressure injected into the tectal representation of the area dorsalis ($n = 7$ left, $n = 5$ right).¹⁴ After 7 days birds were deeply anaesthetized and perfused with 4% PFA. After cryoprotection 35 μ m frozen sections were cut in the frontal plane and processed according to a standard ABC-DAB protocol.¹⁵ At each of coordinates A5.75, A6.25, and A6.75 five randomly chosen square-shaped areas in dorsal ($n = 1$), lateral ($n = 2$) and medial rotundus ($n = 2$) contralateral to the injection side were analysed with a micrometer grid. Using the $\times 40$ objective, each side of the 10×10 grid had an effective length of 20 μ m. The number of labeled axons crossing the lines of the microscopic grid square were counted in each area and summed for each individual. To normalize terminal arbor density in the rotundus with regard to the amount of tracer in deep tectal layers, BDA-labeled perikarya of lamina 13 were counted in every third cresyl violet counterstained tectal section, and using this count as correction factor, the relative number of terminal arbors (see Fig. 3) was calculated.

Results

Results revealed an asymmetry in the number of tectal cells projecting to contralateral rotundus. Labeled neurons crossing from right tectum to left rotundus were about twice as numerous as those crossing from left tectum to right rotundus (t -test, $t_{18} = 3.31$, $p < 0.005$, Fig. 1). There was no significant difference in ipsilateral tectorotundal projections ($t_{18} = 1.4$, ns). A discriminant function analysis with all possibly relevant variables (number of ipsilaterally labeled cells, number of contralaterally labeled cells, injection volume, Euclidean distance of injection tip to stereotaxic coordinates of rotundus core) was run, in order to determine which variables discriminate between left- and right-sided injections. The

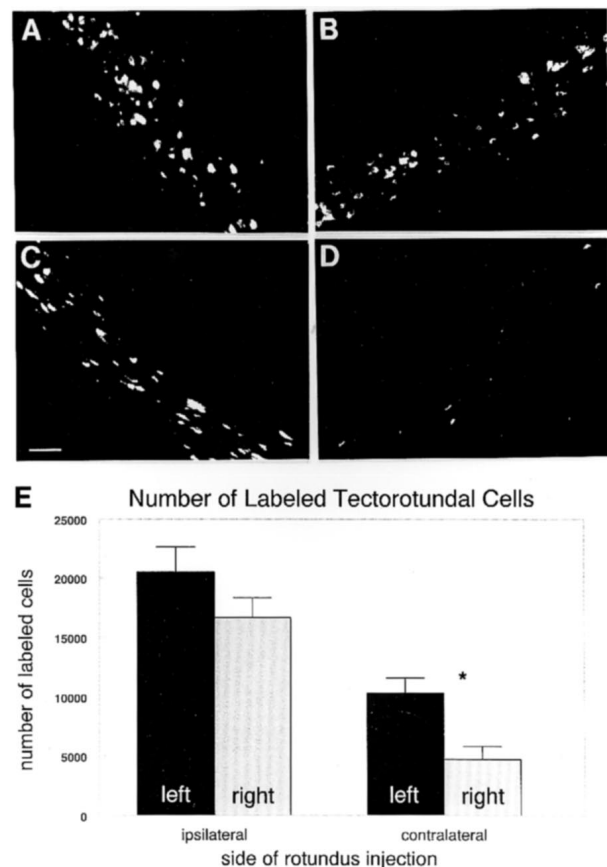


FIG. 1. Frontal sections through the pigeon's tectum opticum after left- (A,C) and right-sided (B,D) rhodamine injections into nucleus rotundus. Labeled cells of tectal lamina 13 in photographs (A) and (B) are ipsilateral, those in (C) and (D) contralateral to the side of rotundus injection. After left or right rotundus injections, more lamina 13 cells are labeled in contralateral right (C) than in contralateral left tectum (D), respectively. Bar = 100 μ m. (E) Number of labeled ipsilateral and contralateral tectal neurons. After left-sided injections, the number of contralaterally labeled cells is significantly higher.

analysis function was significant ($F_{(4,15)} = 3.23$, $p < 0.05$), and only the number of contralaterally labeled cells discriminated between the left-right injection distinction ($F_{(1,13)} = 4.94$, $p < 0.05$, all other variables: $F < 1.1$, ns). The number of contralaterally labeled cells was highly correlated ($r = 0.84$) with the left-right distinction, explaining $> 70\%$ of data variance. Thus, the retrograde tracing experiments revealed a clear and significant asymmetry in the number of contralaterally labeled tectal neurons after rotundus injections which was not due to differences in injection volume or location. The higher bilaterality of left rotundal afferents is shown by the bilaterality index ($BI = n_{\text{ipsi}} - n_{\text{contra}} / n_{\text{ipsi}} + n_{\text{contra}}$) which expresses the degree of bilaterality as a score between minus one (perfectly contralateral) and one (completely ipsilateral). The BI was on average 0.33 for the left but 0.61 for the right rotundus ($t_{18} = -3.14$, $p < 0.01$), indicating a more bilateral input to left rotundus (Fig. 2).

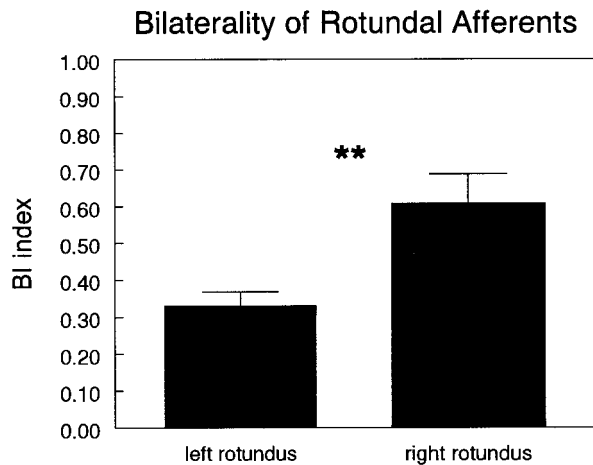


FIG. 2. Bilaterality index (BI) of left and right nucleus rotundus. A BI of 0 indicates perfectly symmetric tectal afferents from both hemispheres, while a BI of 1 denotes a completely ipsilaterally organized system. Tectal input to the left rotundus is significantly more symmetric than visual input to the right rotundus.

Findings were further validated by anterograde tracing of the tectorotundal projection after tectal BDA injections. Since the retrograde tracing study had revealed a significantly higher number of cells projecting from right tectum to left rotundus, we predicted a higher terminal arbor density in contralateral left rotundus than vice versa. This was indeed the case (Fig. 3). The relative contralateral tectorotundal terminal arbor density was significantly higher after right tectal injections (Mann-Whitney U test, one-tailed, $p < 0.05$).

Discussion

Our retrograde tracing data show that left rotundus receives afferents from a higher number of contralateral tectal cells, leading to a higher left-sided terminal density from the contralateral side than *vice versa*, as shown in the anterograde tracing experiments. This asymmetry in ascending visual projections is consistent with behavioral results, showing a right eye/left hemispheric dominance in visual feature detection in pigeons.³ Asymmetries in commissural connections of sensory projections might, therefore, constitute a core aspect of visual lateralization in pigeons. Since each tectum represents the input from the contralateral eye and thus from the contralateral field of view, we suggest that the asymmetrical tectorotundal projection creates a more complete representation of the visual scenery at left rotundal level (Fig. 4). Consistently, unilateral left-sided lesions of the rotundus result in acuity deficits of the right and the left eye while right-sided rotundal lesions only lead to minor visual deficits on contralateral left side.⁸ The rotundus of each hemisphere projects ipsilater-

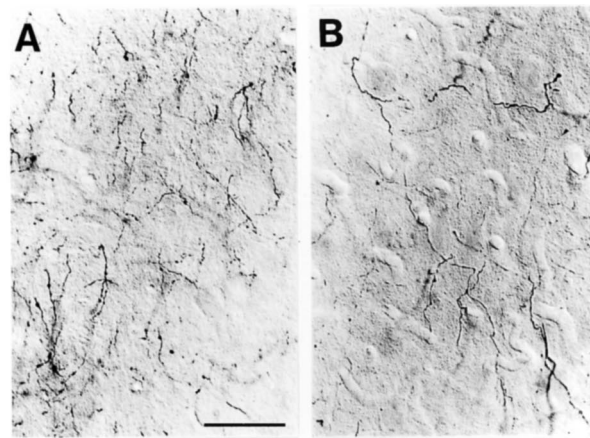


FIG. 3. Frontal sections through left (A) and right (B) nucleus rotundus after contralateral tectal BDA injections. Terminal arbor density is higher in left rotundus. Bar = 50 μ m. (C) Relative number of terminal arbors.

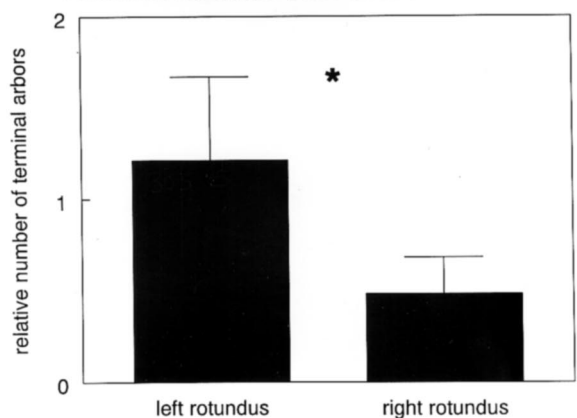


FIG. 3. Frontal sections through left (A) and right (B) nucleus rotundus after contralateral tectal BDA injections. Terminal arbor density is higher in left rotundus. Bar = 50 μ m. (C) Relative number of terminal arbors. After contralateral tectal injections, significantly more arbors are found in left rotundus.

ally to the ectostriatum of the forebrain. Asymmetries established at rotundal level are therefore transposed to telencephalic circuits. The final lateralized visual behavior of the animal then emerges from the interaction of the ectostriatum with forebrain components of the thalamofugal system.

It is conceivable that asymmetrical representations are a general property of lateralizations including those of humans. Several studies have reported that visuospatial attentional tasks are associated with an activation of the dominant right superior parietal lobe after left and right sided attentional shifts, while the subdominant left hemisphere is, if at all, only active while attending to contralateral right stimuli.^{16,17} Consequently, some patients with right parietal lesions neglect target stimuli in both hemifields, while left sided lesions only lead to mild contralateral impairments.¹⁸ A mirror-image pattern is observed for hand motor control. In right-handers, motor areas of the dominant left hemisphere are activated

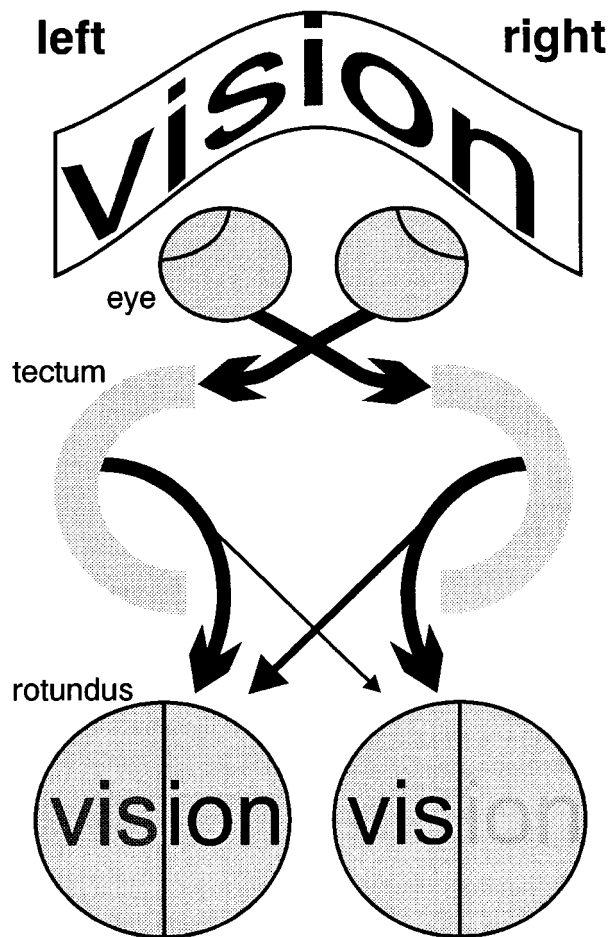


FIG. 4. Schematized view of retinotectal and tectorotundal system in pigeons. The asymmetry of contralateral tectorotundal projections leads to a more complete representation of both visual fields seen by the two eyes in the left hemisphere.

during left and right hand movements, while the subdominant right hemisphere is only involved in left hand motions.^{19–21} In left-handers, the dominant right premotor area is activated after finger movements on either side while left premotor area is only involved in contralateral movements.²² Some right-handed patients with alien hand syndrome and hemispheric disconnection are unable to cross the body midline with left hand, while being able to reach in whatever space position using the right hand.^{23,24} Again, these patterns might be related to a bilateral manual space representation in dominant left motor cortex, while representation is only contralateral in subdominant right motor cortex. Functionally, a complete representation of both sensory hemifields gives the dominant hemisphere instant access to all relevant informations if objects traverse vertical meridian, or when limbs have to be moved beyond body midline. Without such a bilateral representation on the

dominant side, stimuli crossing the midline would probably induce extra processing time due to interactions and coordinations between hemispheres.

Conclusion

In pigeons, visual feature detection is dominated by the left hemisphere. Lesion studies have shown feature detection to be essentially linked to tectofugal information processing. We now show, that the ascending tectorotundal projection is organized asymmetrically with the left hemisphere receiving more bilateral visual input than the right hemisphere. As visual input to the tectum is nearly completely crossed and consequently unilateral, we suggest that the asymmetry in ascending projections results in a more complete representation of the visual scenery within the left hemisphere. Functional asymmetries in visual tasks were shown for a number of species including man. As in all vertebrates input from the hemifields is initially processed within the contralateral hemisphere, integration of visual percepts of both sides must arise from commissural connections. Asymmetries in commissural connections might therefore also account for representational asymmetries of visual percepts shown in humans.

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