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Functional subdivisions of the ascending visual pathways in the pigeon

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Abstract

This study represents an attempt to examine an alternative view of the functional architecture of the ascending visual pathways in pigeons. According to this conception the pars dorsalis (GLd) of the thalamofugal system represents the lateral monocular field of view and is frontally blind to a large extent. The tectofugal system, on the other hand, processes frontal visual input within the framework of asymmetrical tectorotundal connections. As a result, the left, but not the right, rotundus should be able to integrate to an important degree the input from both eyes via the tecta of both hemispheres. Two lesion studies were conducted to test these assumptions. In the first psychophysical experiment, the visual acuity was determined in head-fixed pigeons. After thresholds were determined, stereotaxic lesions were placed in the GLd and/or the rotundus. Multiple regressions between structure specific lesion extents and postoperative threshold alterations demonstrated that only GLd lesions contributed to acuity reductions. In the second experiment the acuity threshold of pigeons under binocular and monocular conditions was determined in a conventional skinner box before GLd and/or rotundus lesions. Multiple regression analyses showed that rotundus- but not GLd lesions contributed to performance losses. The left rotundus lesions were significantly related to threshold elevations under both monocular conditions, while the right rotundus only contributed together with the left rotundus to binocular performance. The double dissociation revealed in these experiments indicates that the ascending pathways in pigeons are functionally segregated and differentially process frontal and lateral as well as left- and right-sided inputs. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Since the pioneering studies of Karten, Hodos, and coworkers, in the 1960s and the 1970s, it has been established that the thalamo- and the tectofugal pathways of birds constitute two parallel ascending visual streams to the forebrain [27,28]. Although it was recognized from the beginning that the parallel nature of these systems might be organized in a modular fashion, pathway-specific functional specializations were hard to reveal since lesion studies were plagued with a rather unexpected problem: most studies were unable to show a substantial contribution of the thalamofugal system to any kind of visual task in pigeons. Lesions of the thalamofugal pathway had little or no effect on the ability to discriminate patterns, intensities, or colors [20], to detect in psychophysical experiments differences in intensity, orientation, or spatial frequency [22,23,29,31], or to master different cognitive tasks [4,6,39]. In contrast, tectofugal lesions severely impaired pigeons in their ability to discriminate even coarse differences in pattern, color, or intensity [20], increased dramatically psychophysically determined thresholds for orientation, size, and intensity discrimination [22,23,29,31], and diminished the capacity of the animals for specific cognitive processes [38]. These results have led to the widespread assumption that, at least in pigeons, the thalamofugal pathway is only of minor importance and that the tectofugal system subserves most if not all components of visually guided behavior.

We wish to propose an alternative view of the pigeon's visual system and its functional architecture. According to this view the visual system is divided

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along the frontolateral distinction of the visual field into a tecto- and a thalamofugally based domain. The tectofugal system is additionally divided along the left–right axes into asymmetrically organized and functionally differing entities. The seemingly parallel organization of the tecto- and the thalamofugal pathway should, according to this hypothesis, be replaced by a neural organization in which the two systems contribute in a modular way to processes which have their domains in different parts of the visual field, and in differing hemispheres.

2. Experiment 1: the frontolateral division of the visual system

2.1. Introduction

Virtually all visual discrimination experiments with pigeons utilize the key peck as the final operant. Birds learn quickly to peck at stimuli projected on pecking keys. In addition, they generally learn easily which stimulus on a pecking key is associated with a food reward. Before pecking, the pigeons observe the stimuli with their frontal visual field [10]. During pecking, frontal stimuli are seen with the dorsotemporal part of the retina, the so-called 'red field' [33]. According to Remy and Güntürkün [34] the red field is only sparsely represented within the n. geniculatus lateralis, pars dorsalis (GLd), the diencephalic relay of the thalamofugal system. The central fovea, however, which looks into the monocular lateral visual field, is densely represented in the GLd. This anatomical condition should make the thalamofugal system frontally blind to a large extent. Thalamofugal lesions are then likely to produce only minor deficits when tested with frontal stimuli. Testing the thalamofugal system should be done in the lateral visual field. Since, on the other hand, the tectum receives a complete representation of the contralateral retina [34], frontal stimuli should be primarily processed by the tectofugal system. The aim of the first experiment is therefore to test the contribution of the two ascending pathways on lateral acuity.

2.2. Method

2.2.1. Subjects

Seven adult pigeons were used. Throughout the experiment, the animals were deprived of water for 24 h before each session. This produced a water deficit of approximately 20 ml. To enable the head of the animals to be fixed to the apparatus, a small rectangular metal block with a tapped hole was fixed to the middle of the skull under anesthesia, and the animals were allowed to recover for 1 week.

2.2.2. Apparatus and procedure

Precise details of the procedure are given in Hahmann and Güntürkün [18]. In summary, the pigeon was held in a cloth bag and its head was fixed in position by screwing the head block to a holder which was connected to a support stand, positioned to one side of the head. The pigeon's beak was positioned in an adjustable water receptacle with an infrared light gate so that beak openings activated the gate, thus triggering an electromagnetic valve permitting water to flow into the receptacle. The average reinforcement was 0.03 ml of water. The water was automatically withdrawn 1.7 s after delivery. The water dispenser and head-block holder did not obstruct the animal's view of the stimuli. The stimuli were projected onto a translucent screen with a slide projector. The stimulus display was located 83 cm from the bird's left eye and subtended a visual angle of about 11°. The projection screen was oriented at a right-angle to the optic axis of the bird's left eye.

The positive stimuli (S +) consisted of high-contrast, square-wave gratings ranging in spatial frequency from 1 to 16 lines/mm. Contrast varied between 0.99 for the lower and 0.95 for the higher frequencies. Luminance of the stimuli ranged from 65.8 to 80.8 cd/m^2. The negative stimulus (S −) was a Kodak Wratten No. 96 neutral-density filter of a nominal optical density of 0.3. The log luminance difference of all stimuli was < 0.03. Differences between pairs of stimuli ranged from 0.005 to 0.026 log units. The testing room was illuminated with two frosted 25 W bulbs located 40 cm diagonally above and behind the animal providing a luminance of 165.4 lx directly below the lamps. The experiment was controlled by a Commodore® 64 computer.

The birds were first trained to discriminate gratings of the lowest spatial frequency (1.0 cycles per degree (c/deg) square wave on the screen) from the matched blank stimulus in a go/no-go design with correction trials. Stimuli were presented to the bird's left eye. Beak openings in the presence of S + resulted in water access and illumination of the water dispenser. Beak openings in the presence of S − were punished by a 10-s time-out period and an error-correction procedure in which the bird had to respond correctly in order to proceed to the next trial. These additional correction trials were not counted. The S + and S − stimuli were alternated according to a quasirandom sequence. After reaching a stable discrimination performance of at least 80% within five consecutive sessions of 50 trials each, the psychophysical testing phase began.

One session was performed daily and consisted of 88 stimuli. A single session always started with 20 trials of the lowest grating frequency (1 c/deg) combined with the corresponding S − . If the performance index was 80% or higher the testing phase began. The following 60 trials were divided in six sequences of 10 trials each in which the 1 c/deg stimulus and one of the higher

Table 1
Left (L%), right (R%), and bilateral (W%) lesion extents of the GLd (thalamofugal) as well as of Rt and T (tectofugal) of the animals tested in experiment 1

Group	Case	Thalamofugal			Tectofugal			VAI	
		L%	R%	W%	L%	R%	W%	VAI_1	VAI_2
GLd	351	11.6	31.4	9.8	0	0	0	−0.45	−0.52
GLd	459	6.9	19.9	1.4	0	0	0	−0.58	−0.53
GLd	461	0	28.7	0	0	0	0	−0.45	−0.51
GLd+Rt+T	352	21.2	53.1	11.3	7.7	21.3	1.6	−0.78	−0.76
GLd+Rt+T	355	99.6	94.8	94.4	90.6	81.8	74.1	−0.89	−0.89
GLd+Rt+T	357	15.5	84.7	13.1	0.4	35.8	0.2	−0.87	−0.87
GLd+Rt+T	367	24.7	92.3	22.8	3.1	76.3	2.4	−0.78	−0.78

Pre- to postoperative acuity alterations are indicated by the VAIs as calculated within 1 month after surgery (VAI_1) and about 3–4 months later (VAI_2).

frequency stimuli (3, 5, 10, 13, and 16 c/deg) were arranged in an ABABAB order. Within each sequence S+ and S− alternated pseudorandomly. The last eight trials consisted again of the 1 c/deg stimulus and its corresponding S−. The visual acuity threshold (75% correct) was determined daily from psychometric functions of choice response accuracy. The pigeons were tested until their performance satisfied the criterion of stability, which was that the mean-detection threshold had to remain within the range of ±15% for five consecutive sessions. The next set of higher grating frequency was then introduced. This procedure continued until performance dropped to chance level.

Following testing, the subjects received diencephalic brain lesions. As outlined above, the GLd represents the diencephalic relay of the thalamofugal system. It receives retinal afferents and projects to the Wulst in the forebrain. The diencephalic relay of the tectofugal system is the n. rotundus (Rt) and the much smaller n. triangularis (T). They receive afferents from the tectum and project to the ectostriatum in the forebrain. Both, the thalamo- and the tectofugal pathways are partly crossed, since the GLd projects bilaterally onto the Wulst [28], while the tectum projects bilaterally onto Rt and T [16]. Therefore it was also conceivable that lesions ipsilateral to the tested eye might have an effect. Consequently, bilateral GLd and Rt+T lesions were made.

Pigeons were anesthetized with equithesin (0.4 ml/100 g body weight) i.m., and their heads were placed in a stereotaxic holder. The skull was penetrated in two places to allow access to the brain, and the electrode was placed according to the pigeon brain atlas of Karten and Hodos [26]. Bilateral electrocoagulation lesions were made in GLd and/or Rt+T from *A* 7.25 to *A* 5.50 with 15 mA for 20 s. The coordinates of the Rt+T lesions were: *A* 5.5, *L* 2.75, *D* 8.50; *A* 6.00, *L* 3.00, *D* 8.25+*D* 9.25; *A* 6.50, *L* 2.75, *D* 9.00; and *A* 6.50, *L* 3.25, *D* 9.00. Those of the Gld lesions were: *A* 6.25, *L* 2.75, *D* 7.75; *A* 6.25, *L* 3.50, *D* 7.75; *A* 6.75, *L* 2.50, *D* 7.50, *A* 6.75, *L* 3.50, *D* 8.00, *A* 7.00, *L* 2.75, *D* 7.50; and *A* 7.25, *L* 3.50, *D* 8.00. The electrodes were stainless-steel pins, insulated with epoxy paint except at the 0.5 mm long tips.

After 1 week of recovery the psychophysical procedures were continued as before until the stability criterion was reached. Two postoperative visual acuity measurements were performed; the first 1 month (post 1) after surgery and the second a further 3 months later (post 2).

After 5 months of postoperative testing the birds were anesthetized and perfused through the left ventricle with 0.9% NaCl (40°C) followed by 4% formaldehyde (4°C). The brains were removed from the skulls, postfixed in a mixture of 4% formaldehyde and 30% sucrose dissolved in 1.2 M phosphate buffer for 48 h, and cut frontally at 30 μm. Every second section was counterstained with cresyl violet. The sections were dehydrated and coverslipped. Two observers (one of them unaware of the behavioral data) examined the brains microscopically for evidence of neuron loss. Lesion locations and extent were estimated in comparison with an intact brain and were reconstructed on frontal atlas plates at 0.25 mm intervals. Lesion volume and percentage of damage to various thalamic nuclei were determined for left (L%) and right (R%) hemisphere. From these data W% was calculated, which is a weighted index of bilateral damage ($W\%$ ($W\% = (L\% \times R\%)/100$) [21]). W% minimizes the influence of asymmetrical lesions on the statistical analysis. All experiments were carried out according to the specifications of German law for the prevention of cruelty to animals.

2.3. Results

The quantitative reconstructions of the GLd and the Rt+T lesions as well as the psychophysical data of the seven subjects under left viewing condition are depicted in Table 1.

Postoperatively none of the animals exhibited motor impairments that could have affected visual acuity performance. Nevertheless, visual acuity (VA) as the mean resolution threshold in c/deg of the left eye decreased considerably within the lateral visual field after surgery. To correlate the pre- to postoperative visual acuity decrease in the lateral field of the left eye with the amount of structure loss within the thalamofugal (GLd) and the tectofugal (Rt and T) pathway of both hemispheres, the visual acuity index (VAI) was calculated as $(VA_{post} - VA_{pre})/(VA_{post} + VA_{pre})$ for each bird and the left viewing condition. VA_{pre} is the mean spatial resolution thresholds of each bird expressed in c/deg for the final five preoperative sessions. VA_{post} gives the comparative measure for either the five postoperative stability sessions 1 month (calculated for VAI_1), or 4–5 months after surgery (calculated for VAI_2). Negative indices indicate a decrease in the postoperative spatial resolution. This was the case in all animals. Three animals were unable to even postoperatively discriminate the 1 c/deg stimuli. Their postoperative performance was estimated by $(1 - (1/\text{preoperative acuity}))$. This is a very conservative index and gives values slightly smaller than 1 c/deg proportional to the preoperative acuity threshold of an animal.

Initial and final VAIs were very close and could not be differentiated statistically. Therefore only VAI_1 was used for the statistical analysis. We ran three separate regression analyses, one for the lesion sizes of the right hemisphere structures, one for those of the left hemisphere, and one for the weighted index of bilateral damage. The overall model fit for the right hemisphere was highly significant ($F(3,4) = 37.68$, $P < 0.01$, $R^2 = 0.97$). Lesion size of the right GLd was the only significant factor ($F(1,6) = 23.64$, $P < 0.01$, $r = -0.88$). Neither the right Rt + T lesion nor interaction of both GLd and Rt + T showed a significant influence on visual acuity performance of the left eye ($F(1,6) < 1$, for both cases). The overall model fit for the left hemisphere was also significant ($F(3,4) = 11.2$, $P < 0.05$, $R^2 = 0.89$). Again, the lesion size of the GLd was the only significant factor ($F(1,6) = 13.23$, $P < 0.05$, $r = -0.63$) and neither the left Rt + T lesion nor the interaction showed a significant influence on left eye acuity ($F(1,6) < 1$, for both cases). Bilateral damage, as expressed by $W\%$, was an insignificant predictor of visual acuity of the left eye, as the overall model fit for the weighted index showed ($F(3,4) = 5.81$, $P = 0.0611$, $R^2 = 0.81$).

2.4. Discussion

This experiment clearly reveals that GLd lesions are significantly related to lateral acuity deficits while, unexpectedly, Rt + T lesions had no impact on the same task. As outlined in the introduction, thalamofugal lesions are known not to impair frontal acuity to an important extent while tectofugal lesions produce severe deficits. Taken together, these studies might indicate that frontal and lateral acuity are subserved by different neural systems.

According to the hypothesis outlined in the introduction, thalamofugal lesions should be expected to cause only lateral deficits since the central retina is represented in the GLd, while the superiotemporal retinal red field is virtually not [34]. The multiple regressions of the present study additionally show that left sided and thus ipsilateral GLd lesions contribute to left eye acuity. The GLd of pigeons projects bilaterally to the forebrain, although the proportion of axons crossing the midline is probably smaller than in owls with their extended frontal vision [28]. The ipsilateral effect of left GLd lesions might therefore be related to these bilateral projections.

Although the central retina, including the fovea, of the pigeon is represented in both the tecto- and the thalamofugal pathways, the present data did not show any significant contribution of Rt + T lesions on lateral acuity. The absence of tectofugal effects is unexpected and has to be cautiously interpreted since only four animals had Rt + T damage. However, if these data hold in future studies they might be interpreted in two alternative ways: either the tectofugal pathway represents the lateral visual field but selectively does not contribute to acuity processes in this area, or the tectofugal pathway does not represent the lateral visual field at all. Indeed, both interpretations could in principle apply. Most neurons of the tectofugal pathway are highly sensitive to motion [24,37], whereas units of the thalamofugal system are characterized by smaller receptive fields and a low adaptation to stimulus repetition [25,30]. Thus, it is conceivable that the tectofugal pathway specializes at least in the lateral visual field to neural processes like, e.g. motion, and contributes only little to spatial resolution. However, it is also possible that the lateral visual field is represented at the tectal but not at the Rt level. Indeed, a recent reanalysis of the tectorotundal pathway with highly selective tracers revealed that, mainly, the ventral tectum representing the lower frontal visual field projects onto Rt [19]. Thus, the absence of a contribution of Rt + T lesions to lateral acuity could be related to an underrepresentation of the lateral field at the Rt and T level.

3. Experiment 2: the left-right division of the tectofugal pathway

3.1. Introduction

Beginning with the pioneering experiments of Rogers and coworkers (for review see Rogers [36]), a large number of studies have shown that the left hemisphere of several avian species seems to be dominant for different visual feature discrimination processes. Visual lateralization in pigeons seems to depend to an important degree on the tectofugal system [12]. The tectum itself displays a number of morphometrical asymmetries with cells up to lamina 12 having larger perikarya on the dominant left side [13]. In addition to the left–right differences of soma sizes, there seems to be an asymmetry in the tectorotundal projections. Neurons of tectal lamina 13 project bilaterally onto Rt and T [1,16]. The bilateral nature of this projection should lead to representations of both the ipsi- and the contralateral eye in the tectofugal system of each hemisphere—a condition shown to be the case by electrophysiological means [7]. Quantifications of tracing data show that the contralateral tectorotundal projection differs by number between left and right: standard injections of the retrograde tracer rhodamine into the Rt of 20 adult pigeons and subsequent counting of labeled cells in the ipsi- and the contralateral tectum revealed asymmetries in the number of labeled cells [11]. While the quantity of ipsilaterally backlabeled tectal neurons did not differ after left or right sided injections, left sided Rt-injections revealed a significantly higher number of backlabeled neurons in the contralateral tectum than after right sided Rt-injections. Thus, the left Rt seems to receive a higher number of inputs from the contralateral tectum, than the right Rt. Since the tecta represent the contralateral visual field of view, the left Rt could integrate both sides of the visual scene to a more complete extent than the right Rt. If this anatomical condition affects functional processes within the ascending tectofugal system, left sided Rt lesions should affect contra- and ipsilateral frontal acuity, while right sided lesions should mainly have an impact on contralateral spatial resolution. As outlined in the beginning, GLd lesions should create no frontal acuity deficits, irrespective of side.

3.2. Method

Twenty 12 months old unsexed homing pigeons of local origin were used. The birds were maintained at 80% of their free-feeding weights during the experiments, with water always available in the home cages. A small metal head block with a tapped hole was glued to the skull with dental cement under anesthesia for the fixing of opaque hemispherical eye caps during monocular discrimination sessions.

The pigeons were trained and tested in a single key operant conditioning box. Stimuli were projected with an external 35 mm slide projector. Positive (S +) and negative (S −) stimuli were the same as in the first experiment. Stimulus luminances ranged from 222.6 to 397.26 cd/m^2. The interior of the pigeon chamber was illuminated by a shielded 1.2 W houselight. The overall chamber illumination was 41.8 cd/m^2. The ceiling luminance varied from 309.4 cd/m^2 directly below the lamp to 6.8 cd/m^2 in the darkest corner.

After autoshaping, an instrumental successive discrimination procedure with correction trials was performed. The acqusition phase started with 20 trials of the 1 c/deg stimulus paired with the matched negative stimulus. Five pecks on the grating stimulus resulted in a 2.5 s grain delivery and additionally illuminated the feeder light within the chamber. Then a new stimulus was presented. The order of stimulus alternations was determined according to a pseudorandom sequence. A peck on the negative stimulus resulted in a 10-s time-out period, during which the chamber and key lights were inoperative. The same stimulus pair was then presented again. The correction trials were repeated until a correct response was made. These additional correction trials were not counted. After reaching 80% correct responses in a single session the psychophysical tests began. Now, 88 instead of 20 stimuli were presented per session. The procedure of testing with these gratings was identical to experiment 1. To calculate the final visual acuity of the pigeons, the mean distance of 58.0 mm from the surface of the gratings to the pupil nodal point was taken (for further technical details see Hahmann and Güntürkün [17]). After having determined the acuity thresholds under binocular conditions, the procedure was repeated under monocular conditions. The animals were tested with the same procedure on alternate sessions with sight restricted to the left or the right eye by means of eyecaps. Finally, the animals were anesthetized and lesioned as explained in the first experiment. Five animals received bilateral, five unilateral left, and five unilateral right Rt + T lesions. Five control pigeons received bilateral GLd ($n = 3$) or sham lesions ($n = 2$). Since two animals died during surgery, the bilateral and right lesioned group consisted of four animals. After 1 week of recovery, the animals were tested for 3 months in the same psychophysical procedure as preoperatively. Then, they were perfused and the lesion volumes were quantitatively reconstructed as outlined in experiment 1.

3.3. Results

The results of the lesion reconstructions and the psychophysical results are outlined for each animal in Table 2.

To correlate the pre- to postoperative visual acuity decrease under binocular, monocular left, and monocular right conditions with the amount of structure loss within GLd (*L*%, *R*%, and *W*%) and Rt + T (*L*%, *R*%, and *W*%) of both hemispheres, the VAI was calculated as in experiment 1. For three animals which were unable to even discriminate postoperatively between the

Table 2
Left (L%), right (R%), and bilateral (W%) lesion extents of the GLd (thalamofugal system) as well as of Rt and T (tectofugal system) of the animals tested in experiment 2

Group	Case	Tectofugal system			Thalamofugal system			VAI		
		L%	R%	W%	L%	R%	W%	VAI-left	VAI-right	VAI-bin
Rt+T left	31	85.9	0	0	98.04	0	0	−0.10	−0.28	0.01
Rt+T left	17	89.92	0	0	89.92	0	0	−0.25	−0.09	0
Rt+T left	21	91.79	0	0	64.4	0	0	−0.20	−0.35	0.33
Rt+T left	5	92.11	0	0	94.91	0	0	−0.30	−0.55	−0.15
Rt+T left	28	36.41	0	0	32.12	0	0	−0.02	−0.14	0.06
Rt+T right	13	0	4.86	0	0	13.43	0	0.24	0.24	0.33
Rt+T right	36	0	38.31	0	0	25.81	0	−0.16	−0.08	0
Rt+T right	6	0	63.71	0	0	88.54	0	−0.1	0.03	0
Rt+T right	20	0	44.29	0	0	34.07	0	−0.13	−0.06	0.04
Rt+T bilateral	3	85.16	99.41	84.66	98.28	100	98.28	−0.86	−0.85	−0.88
Rt+T bilateral	2	52.88	63.57	33.62	83.36	83.53	69.63	−0.05	0.07	0.04
Rt+T bilateral	47	70.67	54.68	38.64	95.93	81.75	78.42	−0.28	−0.76	−0.26
Rt+T bilateral	25	47.09	0	0	71.33	44.4	31.67	−0.08	−0.28	−0.10
GLd bilateral	18	0	23.8	0	44.53	41.63	18.54	0.30	0.16	0.36
GLd bilateral	14	6.96	12.34	0.86	80.56	35.59	28.67	0.11	0.34	0.11
GLd bilateral	15	9.29	25.96	2.41	63.03	33.3	20.99	0.23	0.27	0.19
Sham	7	0	0	0	0	0	0	0.05	0.03	0.08
Sham	0	0	0	0	0	0	0	−0.01	0.22	0.15

Pre- to postoperative acuity alterations are indicated by the VAIs as calculated for the left eye seeing (VAI-left), the right eye seeing (VAI-right), or as tested under binocular conditions (VAI-bin).

1 c/deg grating and the S−, the same estimation procedure as outlined in the first experiment was used. Multiple regression analyses which were calculated independently for the VAIs of the binocular, monocular right, and monocular left conditions revealed a substantial contribution of tectofugal structures and a complete absence of thalamofugal effects. The overall analysis of the binocular data set was significant ($F(6,12) = 4.08$, $P < 0.02$, $R^2 = 0.67$) and only bilateral Rt + T lesions contributed significantly to the dependent variable ($t(12) = -2.29$, $P < 005$). The regression coefficients between bilateral Rt + T lesion volumes and VAIs was very high ($\beta = -1.95$, $r = -0.82$). The overall model fit for the results gathered under monocular right conditions was also significant ($F(6,12) = 6.6$, $P < 0.005$, $R^2 = 0.77$) but in this case only left Rt + T was the significant factor ($t(12) = -2.86$, $P < 0.05$) with high regression coefficients ($\beta = -1.4$, $r = -0.76$). For the VAIs under monocular left conditions the overall model fit was highly significant ($F(6,12) = 10.19$, $P < 0.001$, $R^2 = 0.84$). The lesion size of left Rt + T was again the only significant factor ($t(12) = -2.19$, $P < 0.05$, $\beta = -0.9$, $r = -0.66$).

3.4. Discussion

The results of the present experiment clearly reveal that Rt- and T- lesions have asymmetric impacts on frontal acuity. As predicted, left-sided damages had ipsi- and contralateral effects, while right-sided tectofugal lesions contributed only together with the left side to a reduction of binocular performance. As shown in several previous studies, thalamofugal damage had no influence on frontal acuity.

The fact that bilateral diencephalic tectofugal but not thalamofugal lesions attenuate frontal acuity has been previously shown by Macko and Hodos [29]. The present data thus agree with their results exactly. It is likely that the differential representation of the superiotemporal retinal red field in the tectum and the GLd is the anatomical basis for this difference between tecto- and thalamofugal effects [34]. Thus, the present data add further evidence to the observation that thalamofugal lesions have no or at least minor effects on frontal visual performance.

The contribution of the left and the right Rt and T lesions were substantially different. While the left sided lesions had effects on ipsi- and contralateral acuity, those of the right side did not significantly diminish monocular performance. This asymmetry is, in general, consistence with the hypothesis outlined in the introduction. It confirms with behavioral techniques the anatomical data which would make it likely that it is mainly the left Rt which represents the input of the contra- and the ipsilateral eyes [11]. It also perfectly accords with previous data in pigeons which could show that lesions of the telencephalotectal tracts of only the left hemisphere attenuate visual discrimination performance [15].

Contrary to the previous prediction, the right sided Rt and T lesions had no effect on contralateral left acuity. There is no doubt that a massive ipsilateral tectorotundal projection leads from the right tectum to the right Rt. It is also clear that most cells in the right Rt respond to stimuli in the contralateral left visual field. So the question is, why right Rt lesions did not attenuate left eye acuity. It is in principle conceivable that the left and right Rt not only differ in the degree of ipsilateral representation but also in the mode of processing. Data from different avian species show that spatial cues are more efficiently processed by the left eye/right hemisphere [12,36]. Thus, the absence of right Rt lesion effects on left eye acuity might be related to the fact that the animals were tested for acuity and not for spatial discrimination.

4. General discussion

The two lesion studies outlined in the present paper reveal important functional segmentations in the ascending visual pathways of the pigeon. The first experiment shows that the division between frontal and lateral seeing is, at least for acuity, also a division between tecto- and thalamofugal mechanisms, respectively. The second experiment reveals that left Rt is able to process most relevant aspects of the acuity task, while the contribution of the right side is rather negligible. Fig. 1 depicts a schematic view of the functional architecture which might emerge from these results. With the present state of knowledge an interpretation of these data, as outlined in the following paragraphs, can not obviously be more than speculative.

In experiment 1, the starting point was the difference in the projections of the retinal subfields to the GLd and tectum. The anatomical study of Remy and Güntürkün [34] had shown that the superiotemporal 'fovea' subserving frontal vision was only represented to a limited extent in the GLd. This is in contrast to studies from some birds of prey, in which the temporal, but not the central retina projects to the GLd [2,3], while the complete retina projects onto the tectum. Thus, pigeons and some birds of prey follow the principle that the tectum receives input from the complete visual field while the GLd specializes. However, the GLd specializes in different fields of view in pigeons and birds of prey.

It is conceivable that differences in visual scanning and feeding mechanisms could explain these differences at least in part. Pigeons fixate complex and distant stimuli laterally and only switch to frontal vision to peck the scrutinized object [9]. This frontal 'pecking field' is myopic, like the whole inferior parts of the eye [8]. Thus, visual detection and analysis of most distant objects which require fine analysis is mainly performed by thalamofugal mechanisms looking laterally. Electrophysiological recordings generally demonstrate neurons with small stationary receptive fields within the GLd and Wulst [25,30]. This fits to the observation that the acuity of the lateral field is considerably higher, compared with the frontal field tested under monocular conditions [14,18]. On the other hand, the frontal specialization of the thalamofugal system in some birds of prey might be related to their more complex feeding habits which require them to specify the distance of objects with great precision while moving at high speed. This is probably achieved through depth cues such as binocular disparity or through flow-field variables [5]. Although eagles and falcons fixate distant objects mainly laterally they switch to frontal vision when approaching prey [35]. The combination of high frontal acuity [35] without lower field myopia [32] together with the need for complex and fast visual information analysis might explain the specialization of the thalamofugal pathway in the frontal visual field in birds of prey.

The different importance of Rt and T of the two hemispheres for left and right eye acuity might be

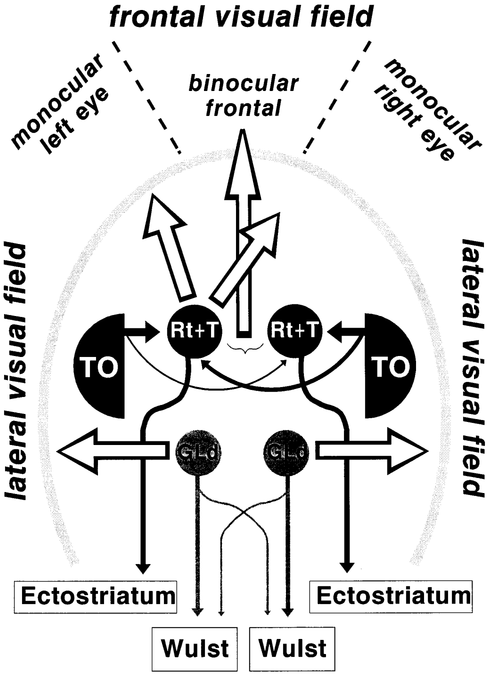

Fig. 1. Schematic depiction of the functional architecture emerging from the present lesion experiments. The grey arch represents the extent of the visual field of a pigeon with its subdivisions in the frontal and lateral components subserved by the left and the right eye. In a highly reduced manner the principle connections of the thalamo- (dark grey) and the tectofugal (black) system is shown. The present study shows that the GLd processes lateral acuity (open arrows pointing sideways). Rt + T of the left hemisphere primarily process monocular frontal left and monocular frontal right eye acuity. Only when tested under binocular conditions, a combined contribution of Rt and T of both hemispheres could be revealed.

related to the specialization of the two hemispheres in different aspects of vision. Avian left hemisphere processes seem to be more related to visual feature identification and categorization, while the right hemisphere is involved in spatial analysis [12,36]. Within this framework it is not unexpected to reveal a significant performance reduction in the discrimination of gratings after left-, but not right-sided lesions. At the same time, this pattern of lesion induced deficits follows, at least in part, the pattern of asymmetric tectorotundal projections which enable a more complete bilateral visual integration on the left side. It is conceivable that this asymmetry of representation is related to the asymmetry of function, and future studies have to show what the nature of this relation is.

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