ELSEVIER

Behavioural Brain Research 134 (2002) 149–156

BEHAVIOURAL BRAIN RESEARCH

www.elsevier.com/locate/bbr

Research report

Embryonic light stimulation induces different asymmetries in visuoperceptual and visuomotor pathways of pigeons

Martina Skiba, Bettina Diekamp, Onur Güntürkün *

AE Biopsychologie, Fakultät für Psychologie, Ruhr-Universität Bochum, GAFO 05/618, 44780 Bochum, Germany

Received 30 August 2001; received in revised form 27 November 2001; accepted 27 November 2001

Abstract

In birds, visual object discrimination performance is lateralized with a dominance of the right eye/left hemisphere. This asymmetry is induced by embryonic light stimulation. However, visually guided behavior, even during simple object distinction tasks, is composed of different behavioral and neural modules. Therefore, the aim of the present study was to test whether all neural subsystems involved in visual discriminations are lateralized in a similar way after prehatch visual stimulation. To examine this question, two behavioral paradigms were used which reveal complementary aspects of visually guided behavior. The first was the grain–grit discrimination task in which no left–right differences in the number of pecks, but significant differences in the number of grains can be found. Therefore, grain–grit discrimination reveals visuoperceptual performance but not visuomotor speed. The contrary seems to be the case for a successive pattern discrimination with a VR32 schedule. Here, the hemispheres do not differ with respect to discrimination accuracy but with regard to the number of pecks emitted. Thus, successive pattern discrimination with lean VR schedules reveals hemispheric differences in visuomotor speed without testing visuoperceptual performance. Using these two paradigms a group of light and a group of dark incubated pigeons were tested. The results show that dark incubated birds evinced no asymmetry in any measure while light incubated ones were right-eye dominant in both variables. However, light incubation induced a visual left hemispheric dominance by modulating two different processes, a left-hemispheric increase of visuoperceptual processes; and a right-hemispheric decrease for visuomotor speed. Taken together these data show that embryonic light stimulation elicits visual lateralization by differently modulating visuoperceptual and visuomotor systems in both hemispheres.

Keywords: Birds; Tectofugal pathway; Tectum opticum; Visual discrimination; Light–dark incubation; Cerebral asymmetries

1. Introduction

The avian visual system is asymmetrically organized. Studies in various avian species revealed a superiority of the right eye for experiments which require the birds to distinguish between different visual objects [7,18,31,42], to memorize hundreds of abstract patterns [6], or to infer a higher-order rule from serial visual color reversals [2]. If using object-cues or absolute distance measures during orientation in small-scale [32,40] or large-scale environments [41] chicks and pigeons also reach higher levels of performance when viewing with the right eye. In contrast, their left eye system predominantly responds to geometry-based topographical cues and has an advantage for social recognition [40,42]. Since optic fibers cross completely at the optic chiasm, these behavioral asymmetries probably arise due to a cerebral dominance of the contralateral hemisphere for the tasks tested.

There is strong evidence, that the behavioral left–right differences closely correlate with neuroanatomical asymmetries of the two major ascending visual projections: the tectofugal and the thalamofugal pathway. These projections are known to correspond, respectively, to the extrageniculocortical and the geniculocortical systems in mammals [12]. In chicks an asymmetrical organization of the thalamofugal pathway has been reported with more projections from the left thalamus to the right visual forebrain, than vice versa

* Corresponding author. Tel.: +49-234-322-6213; fax: +49-234-3214-4377

E-mail address: onur.guentuerkuen@ruhr-uni-bochum.de (O. Güntürkün).

0166-4328/02/$ - see front matter
PII: S0166-4328(01)00463-6

[37]. In pigeons, structural asymmetries of the tectofugal pathway have been found with morphological differences between left and right tectofugal structures [11,26–28], a higher degree of bilateral representation on the left side of the tectofugal pathway [15], and a prominent left–right difference in the transcommissural interactions over midbrain commissures [24].

A considerable number of studies report that in chicks and pigeons visual lateralization is triggered by light exposure of the embryo in the egg shortly before hatch. Avian embryos take an asymmetrical posture with the head being turned to the right such that the right eye receives proportionately more light through the translucent shell, while the left eye is covered by the body [25]. This asymmetrical light stimulation is effective to modulate synaptic patterns of the ascending pathways during a short time window prior to and shortly after hatching. If birds are incubated and hatched under dark conditions, the usual lateralization pattern disappears [10,33]. The direction of lateralization can even be reversed by experimentally closing the right eye to light shortly before hatch in chicks [34] or thereafter in pigeons [27]. Together with the behavioral asymmetries, also the anatomical left–right differences can be reversed or altered depending on the experimental manipulations of the light stimulation. These experimental interventions have to be performed before hatch in chicks and thereafter in pigeons [10,26,27,35,36].

Light stimulation asymmetry during early ontogeny could induce a left hemisphere dominance for object discrimination by increasing performance of left hemisphere processes, by decreasing those of the right, or by differently adjusting distinct neural circuits on both sides. We tested these alternatives by testing dark- and light incubated pigeons in two visual experiments which both yield a right eye advantage but probably tap different kinds of visual processes. One of them was grit–grain discrimination in which the animals have to peck within 30 s, a small number of grains from a trough filled with grit resembling the grains in color and shape [17]. Since not the number of pecks, but the number of grains eaten differs between left and right monocular conditions, visual asymmetry as tested in grain–grit discrimination seems to largely depend on the discrimination accuracy and not on visuomotor speed [17,27]. This is different from successive pattern discriminations using lean variable ratio schedules like VR32 [9]. Here, the animals have to distinguish the correct pattern right at the beginning of a trial, but their reinforcement success largely depends on their speed of pecking. Consequently, their right eye superiority is due to the number of pecks emitted, while the two monocular conditions generally do not differ with respect to the discrimination scores [9,13,16,18]. Thus, pattern discrimination with these VR schedules seems mainly to disclose an asymmetry in visuomotor speed.

Using these two behavioral paradigms, we, therefore, aimed to analyze how embryonic light stimulation influences visuoperceptual and visuomotor processes and thereby affects visual lateralization.

2. Methods

2.1. Animals and incubation conditions

Fertilized eggs from eight pairs of breeding homing pigeons (*Columba livia*) were incubated in two still-air incubators adjusted at the same temperature (38.3 °C) and humidity (60–75%) but varying with regard to their light conditions. One of them permanently received external neon light through an acrylic glass window whereas the counterpart was opaque and kept in darkness throughout the entire period of incubation. Since pigeons usually lay two eggs within 48 h, each was treated disparately to balance genetic influences. The intensity of illumination at the level of the eggs was 196 lx as measured with a EE&G 450 photometer. The eggs were turned automatically and could be inspected easily (light condition) or with a dimmed torch not pointed onto the shell but past it (dark condition). After hatching, the nestlings were banded and swapped with the corresponding artificial eggs the breeding birds were sitting on. There were a total of 11 birds remaining alive until adulthood (seven dark-incubated and four light-incubated birds) which could be taken over into the behavioral tests. In addition there was a smaller group of birds (four dark, four light incubated) which were tested identically in a preliminary, previous study [10]. Although both a grain–grit and a successive pattern discrimination task had been conducted in this former experiment, only the results of the first behavioral procedure had been reported. Since, therefore, the pigeons had been treated and tested in an identical way, the two data sets were pooled to constitute a group of 11 dark- and eight light-incubated pigeons.

2.2. Grit–grain discrimination

Prior to the actual discrimination test the animals were anesthetized with Equithesin (0.4 ml/100 g bodyweight) and the scalp was incised along the midline. A small metal block with a thread was attached to the skull with dental cement. This device served as a mounting for eye caps which could be fitted with a little screw during monocular tests and removed again subsequently. Over the following 5 days of recovery the pigeons had free access to food and water and were then food deprived and maintained on 80% of their natural body weight.

The grit–grain discrimination test required the birds to select small grains of common vetch (*Vicia sativa*) from pebbles of similar size (3–4 mm length), shape, and

color range. For this we used 30 grains and 30 g of pebbles (about 1000 in number) mixed in a tray and attached to the inside of their home cages. After an interval of 30 s starting from the first peck, the mixture was removed again. Two parameters were considered. First, the number of grains swallowed by the bird (calculated by the remaining grains in the grit) and second, the total number of pecks performed within the given period. We determined the index of percent discrimination accuracy by, number of swallowed grains × 100/number of pecks.

After getting used to the task, each pigeon performed the test alternatingly under left and right monocular conditions. The animals completed 20 trials altogether (ten of each seeing condition) and were tested once a day.

2.3. Successive pattern discrimination

The pigeons were trained in a standard skinner box with a single translucent response key which could be illuminated. A food-hopper placed below the pecking key was operated by means of a solenoid switch. A food reward went along with a reinforcement light that lit up simultaneously. The chamber was illuminated by a house light. All relevant events were programmed with digital modular equipment which also counted the key pecking responses. The animals were trained in an autoshaping procedure to peck the key during the response time (key lit) and to avoid pecking it during intertrial intervals (key dark). After reaching criterion of 85% correct pecks in three sessions in row, they started with the successive pattern discrimination training. This also took place in a skinner box with a single response key onto which stimuli were back-projected with a microprojector. The position of the food hopper as well as those of the food and the house light were identical to the first box. One experimental session consisted of 40 trials. Using quasi-random sequences of Gellerman [8], a triangle (S−) and a circle (S+) were presented 20 times each for 20 s. Pecks to the correct stimulus were reinforced by food for 3 s. During that period the key lights vanished. A peck on the negative pattern resulted in an extended S− presentation for 2 s per peck. Pecks during this extension period were registered but not taken into consideration for the calculation of the percent correct score of the animals. The experimental design started with a fixed ratio schedule (FR 1) but switched to a variable ratio schedule (VR 4) as soon as the birds reached or passed the 85% discrimination criterion in three consecutive sessions. After successively meeting the same criterion, the schedule was stepwise increased to VR8, VR16, and finally VR 32. Again, after completion of three consecutive sessions with at least 85% correct choices, monocular tests at the VR 32 level were conducted using eyecaps. Alternating between left and right monocular conditions, the birds had to finish 20 sessions (ten for each monocular condition). The critical dependent variables were the percent discrimination scores (number of pecks on correct pattern × 100/number of pecks on incorrect pattern) and the total number of pecks (correct + incorrect).

2.4. Neuroanatomy

After completion of the behavioral part, the animals were anesthetized with Ketamine and Rompun (40 mg/kg bodyweight each, i.m.) and perfused through the left cardiac ventricle with 0.9% NaCl (40 °C) followed by fixative (4% paraformaldehyde in 0.1 M phosphate buffer (4 °C, pH 7.2)). The brains were removed and kept in 4% phosphate buffer by adding 30% sucrose for 24 h at 4 °C and cryosectioned subsequently in frontal plane (30 μm). The slides were stained with cresylviolet and covered.

The avian optic tectum consists of 15 layers from which the first superficial one is a fiber layer through which axons from incoming retinal ganglion cells pass. The morphometric study of perikarya cross section sizes were conducted for the layers 2–13 which constitute those laminae which receive retinal input and project to the nucleus rotundus—the next pathway of the tectofugal pathway. In each animal and hemisphere, only the dorsolateral tectal section around the most lateral tip of the tectal ventricle at stereotaxic level A 3.75 (Karten and Hodos, 1967) were analyzed. The cross-sectional soma area of 50 neurons from each of laminae 2–13 and each side were measured. Thus, a total of 22 800 tectal neurons (19 birds × two hemispheres × 12 layers × 50 cells) were analyzed. In a previous analysis, several sample sizes from 20 to 300 neurons of lamina 13 had shown that the analysis of 50 cells is sufficient to yield a mean, close to the average of 300 neurons (within 5% of the standard error (S.E.)). Only neurons containing a clear nucleolus, a round and light-colored nucleus and visible Nissl substance in the cytoplasm were considered. A display of these cells was obtained with a Kappa CF8 camera attached to an Olympus BH-2 microscope with a × 100 objective. With an image analyzing system ('Analysis' SIS, Münster) the boundaries of the cells could be encircled by tracking the image displayed on the video screen with a computer mouse. After an appropriate section of a layer was focused each soma within the boundaries of the monitor screen was measured to make sure all types of cells were considered. Layers with low cell densities required a slight shift of the microscope stage to the directly adjacent portion of the tectal section. This procedure was repeated until the sufficient number of neurons had been recorded.

3. Results

3.1. Grain–grit discrimination

A multivariate analysis of variance (MANOVA) of the pecking frequency and the discrimination accuracy with group (light/dark) as a between-subjects factor and seeing condition (left eye/right eye) as a within-subjects factor was calculated. For the pecking frequency no significant main effect for group ($F(1,17) = 0.23$, $P > 0.60$) or for seing condition ($F(2,34) = 2.22$, $P > 0.10$) could be revealed. There was additionally no significant interaction ($F(1,17) = 0.06$, $P > 0.80$). Thus, visuomotor speed did nor differ between groups or monocular conditions.

The analysis of discrimination accuracy revealed no significant group effect between light and dark incubated animals ($F(1,17) = 2.39$, $P > 0.10$), but a main effect of hemisphere ($F(1,17) = 28.70$, $P < 0.001$) and an interaction between group and hemisphere ($F(1,17) = 21.44$, $P < 0.001$). The light incubated pigeons showed a significant right eye dominance (Tukey's HSD test; $P < 0.05$), while there was no left–right difference for dark incubated birds (Tukey's HSD, $P = 0.98$). As shown in Fig. 1, the right eye performance of light incubated pigeons was higher than for all other conditions. Consequently, the left-eye discrimination levels of dark and light incubated animals did not differ (Tukey's HSD, $P = 0.99$) while the right-eye performance was significantly higher in light than in dark incubated birds (Tukey's HSD, $P < 0.02$).

Taken together, in light incubated animals behavioral asymmetry in visual discrimination accuracy was due to an increase of right-eye performance.

3.2. Successive pattern discrimination

In the pattern discrimination test we only used data sets of nine dark and seven light incubated birds, since three animals did not reach criterion despite intense training or had died before they could start with this experiment. The non-achievers did not had to be excluded due to problems with the discrimination as such but due to their reluctance to perform with the lean VR schedule.

Both groups, regardless of which eye was covered, achieved an average score of 98% accuracy, pointing to the ease with which the patterns could be distinguished by the animals. A MANOVA of the discrimination accuracy with group (light/dark) as a between-subjects factor and seing condition (left eye/right eye) as a within-subjects factor was calculated. For accuracy no significant main effect for group ($F(1,14) = 0.78$, $P > 0.38$) or for seing condition ($F(1,14) = 0.10$, $P > 0.75$) could be revealed. Additionally there was no significant interaction ($F(1,14) = 0.10$, $P > 0.75$). Thus, discrimination accuracy did not differ between groups or monocular conditions.

A MANOVA of the number of pecks within one session revealed no main effect of group ($F(1,14) = 0.33$, $P > 0.50$), but significant effects of hemisphere ($F(1,14) = 14.0$, $P < 0.01$) as well as a significant interaction of group and hemisphere ($F(1,14) = 12.2$, $P < 0.01$). A post hoc test (Tukey's HSD) showed that for the light-incubated animals left and right eye seeing conditions differed significantly with a superiority of the right eye ($P < 0.01$). Dark incubated animals yielded no left–right eye differences in their performances. As shown in Fig. 2, the left eye performance of light

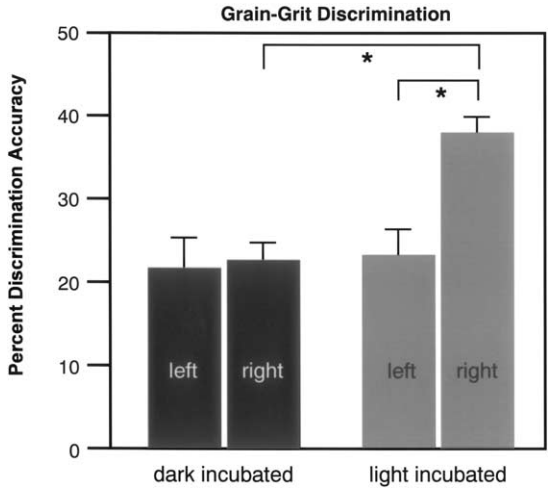

Fig. 1. Mean percent discrimination accuracies of dark and light incubated birds using their left or their right eye in the grain–grit discrimination. Note that the asymmetry of the light incubated animals is due to an increase of right eye performance. Asterisk denotes significance at 5%-level, standard errors (S.E.) are indicated.

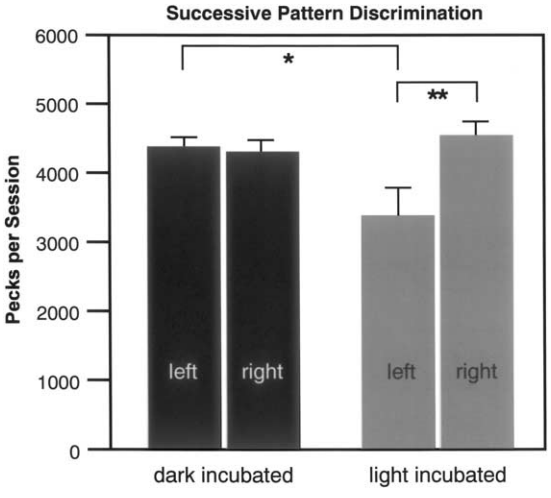

Fig. 2. Mean pecks per session of dark and light incubated birds using their left or their right eye in the successive pattern discrimination. Note that the asymmetry of the light incubated animals is due to an decrease of left eye performance. Single asterisk denotes significance at 5%, double asterisk at 1%-level, S.E. are indicated.

incubated pigeons was lower than for all other conditions. Consequently, right-eye discrimination levels of dark and light incubated animals did not differ (Tukey's HSD, $P = 0.80$) while the left-eye performance was significantly lower in light than in dark incubated birds (Tukey's HSD, $P < 0.05$).

Taken together, in light incubated animals behavioral asymmetry in visuomotor speed was due to a reduction of left-eye performance.

To visualize the extent of behavioral asymmetry for each pigeon, the asymmetry index (AI) was calculated for the grain–grit and the pattern discrimination task as follows:

$$\mathrm{AI} = (\text{performance right} - \text{performance left})/(\text{performance right} + \text{performance left})$$

The measure of performance was the average discrimination accuracy in the grain-grit and the average sum of pecks in the pattern discrimination task. AI can vary between -1 and $+1$. Negative values indicate a left eye superiority, 0 gives a symmetrical performance, and positive values indicates an asymmetry favoring the right eye. As shown in Fig. 3, light incubation shifted the group scatter in direction of a right eye dominance. The extents of these AI-scatters measured in standard deviations were not systematically different between the dark (grain–grit, 0.172; pattern discrimination, 0.075) and the light incubated animals (grain–grit, 0.114; pattern discrimination, 0.105). This makes it likely that dark incubated animals were not constituted by a left- and right-eye dominant group of about equal size, but instead oscillated around 0.

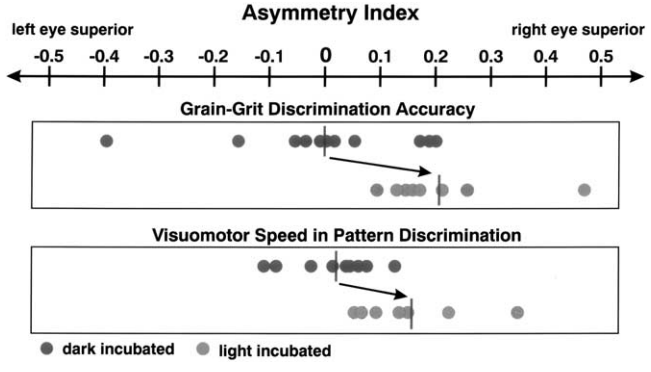

Fig. 3. Individual asymmetry indices of dark and light incubated animals for their grain–grit discrimination accuracy and their visuomotor speed in the successive pattern discrimination task. Note that light incubation shifts the performance into the direction of right eye superiority.

3.3. Neuroanatomy

A comparison of cell soma sizes in single layers of left and right tectum revealed asymmetries of various extents. In order to better compare these data, the tectal layers were grouped according to the following scheme:

- Layers 2–7 were grouped as those retinorecipient layers, where retinal fibers terminate [1].
- Layers 8–12 were grouped as those retinoreceptive layers, which receive direct retinal input by ascending dendrites without projecting to the nucleus rotundus [19].
- Layer 13 was separately analyzed since it constitutes the projection lamina to the rotundus [20].

Left–right differences in tectal soma size between groups were analyzed performing a three-factorial MANOVA (group × hemisphere × layer). This analysis revealed no overall effect of incubation method ($F(1,13) = 0.009$) or of hemisphere ($F(1,13) = 0.974$) on the soma size. Instead, soma size only depended on the three groups of layers ($F(2,26) = 200.62$; $P < 0.001$). All interactions between these factors yielded no significant results (all P's > 0.06). Separate planned comparisons for each group of layer and incubation group on the soma size differences between the left and right hemisphere revealed a significant difference for the soma size of the left versus right hemisphere in layer 13 of light incubated animals ($P < 0.03$). To make the extent of the asymmetry for each group of layers visible, the percent soma size differences between left and right was calculated separately for each animal and layer by taking the soma mean of both sides as 100%. Larger profiles on the left side resulted in negative percent values while larger cross section areas on the right side gave positive percentages. These percent values were

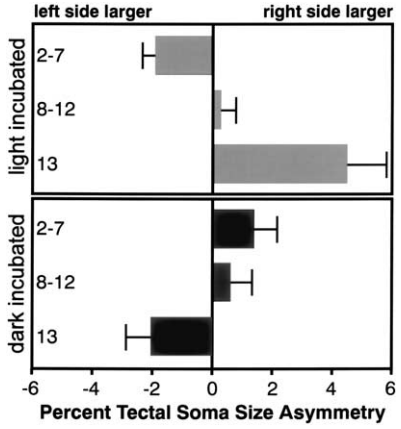

Fig. 4. Mean percent tectal soma size asymmetries of dark and light incubated animals for laminae 2–7, 8–12, and 13. Left-skewed bars indicate larger somata on the left, while a right-skew is indicative for larger perikarya on the right. S.E. are indicated.

then averaged over all animals separately for each group of layers. (Fig. 4).

4. Discussion

The present study clearly shows that visual asymmetry in discrimination tasks is induced by embryonic light stimulation in pigeons. Thus, this is a substantiation of a preliminary study in pigeons [10] and a replication of similar experiments in chicks [33,34]. This light incubation-induced visual lateralization is very likely the result of a prehatch asymmetrical stimulation of the eyes, which is the consequence of the asymmetrical posture of avian embryos before hatch.

All light incubated animals revealed a pronounced right eye/left hemisphere dominance in both behavioral testing paradigms. A closer look at the results, however, reveals that in the grit–grain task the marked right eye dominance in light incubated animals seems to be related to a selective enhancement of left hemispheric performance. In contrast, in the pattern discrimination test the right eye superiority follows from a decrease of the right hemisphere performance. As outlined above, the grain–grit and the successive discrimination task have the potential to specifically tease out different features of visually guided behavior, probably driven by divergent neuronal circuits. As in previous experiments [17,27], the grain–grit test yielded higher pecking accuracies with the right eye, which in turn led to consumption of more food grains. The number of countable pecks, a reliable indicator for motor speed, did not vary between the two seeing conditions. Therefore, the grain–grit task mainly seems to test perceptual processes without high demands on motor speed. The successive pattern discrimination with a VR32 schedule is exactly complementary. Here, reinforcement success largely depends on the speed of pecking. Of course, two highly dissimilar patterns have to be distinguished right at the beginning of a trial, but given the excellent perceptual and visuomnemonic capacities of pigeons, this aspect seems to come easy for the birds [5,38]. Consequently, their right eye superiority was due to the number of pecks emitted, while the two monocular conditions did not differ with respect to the discrimination scores. This is identical to previous experiments [9,13,16,18]. Thus, pattern discrimination with high VR schedules seems mainly to visualize an asymmetry in visuomotor speed. Taken together, light incubation seems to induce a visual left hemispheric dominance by modulating two different processes:

1. an increase of the capacity of the left hemisphere for visuoperceptual processes, and;
2. a decrease of the right hemispheric capacity for visuomotor speed.

This conclusion implies that the effects of embryonic light stimulation are not restricted to a simple unihemispheric enhancement of visual processing, but involve mechanisms selectively supporting some neural circuits in one hemisphere or inhibiting other systems in the other. Indeed, several recent experiments show that asymmetrical light stimulation results in cellular alterations in both hemispheres. Manns and Güntürkün [28] studied tectal GABA- and Parvalbumin-neurons (PV) and revealed that both cellular populations develop asymmetrical soma sizes only after embryonic light stimulation while dark incubation prevents the establishment of left–right differences. However, light engenders a significant size decrease of GABA-cells in the right tectum while it induces a significant shrinkage of PV-cells in the left tectal hemisphere. Since these neurons probably participate in different neuronal circuits, visual asymmetry is established by differently altering both left- and right-tectal systems.

In pigeons, visual lateralization depends largely on left–right differences within the tectofugal system. Consequently, the tectum displays a complex pattern of morphological asymmetries [11]. The tectum is also known to have ascending and descending projections which participate in perceptual and motor processes, respectively. The ascending projections lead via the thalamic nucleus rotundus to the ectostriatum in the forebrain. Lesions of these structures result in severe reductions of visuoperceptual processes without affecting motor behavior [4,14]. Descending projections arising from the tectum topographically innervate premotor hindbrain regions, involved in movement control of eyes and head [30,39]. Stimulation of these pathways elicits complex and spatially organized rapid head movements [3]. A recent study clearly shows ascending and descending projections to arise from completely separated tectal cell groups [21]. According to the present data these separate ascending and descending tectofugal streams are probably differently modulated by an asymmetrical embryonic light stimulation.

According to previous experiments control birds or light incubated animals display larger somata in the retinorecipient layers of the left tectum and larger cells in the right-sided lamina 13 [10,27]. It is conceivable that this rightskew of lamina 13 neurons is due to their more numerous contralateral projections which results in a higher bilateral representation in the left rotundus [14,15]. The light incubated pigeons of the present study evinced the same pattern, although, due to the small sample, the difference to the dark incubated birds reached only significance for lamina 13. However, despite this limitation for the retinorecipient laminae, the present experiment makes it likely that embryonic light stimulation not only induces behavioral but also morphological asymmetries at the tectal level.

The present study shows that dark incubated animals were not lateralized at the population level. They also seem not to be lateralized at the individual level since in both measures the asymmetry indices of the dark incubated birds oscillated around 0 and were thus not constituted by a strong left- and a strong right-eyed group of about equal size. Obviously, some dark incubated pigeons had left- or right-sided asymmetry indices of similar extent as the light incubated animals. Since, however, the standard deviations of both measures were not systematically larger in the dark compared with the light incubated group, it seems to be more parsimonious to assume that dark incubated pigeons constitute a single, non-lateralized group. In this case, light incubation would indeed induce the onset of visual asymmetry. The situation in chicks seems to be different for some measures. Several studies make it likely that asymmetry of imprinting seems to be genetically prewired in chicks and to also occur in dark incubated animals. For example, glutamate NMDA-receptor binding is two-fold higher in the right intermediate medial hyperstriatum ventrale (IMHV) than in the left [23]. The IMHV is a forebrain area which is crucial for imprinting and other early learning processes. Consequently, imprinting seems to be mainly mediated by right forebrain mechanisms [21]. If, however, chicks are asymmetrically exposed to light before hatch, imprinting is mediated by the hemisphere which was visually stimulated [22]. Similarly, dark incubated chicks prevalently show right-hemispheric sleep patterns, while light incubated individuals shift to left-hemispheric sleeping bouts [29]. These example make it likely that some asymmetries can be altered by lateralized embryonic stimulation, but they don't need prehatch light to be established. Visual object lateralization in pigeons, however, seems indeed to be de novo induced by prehatching light. Indeed pigeons always leave their nest under natural conditions about 10–20 times per day. Each of these moves only lasts a short while, but adds to about 30 min per day—a time frame sufficient to induce visual asymmetry (unpublished observations).

Taken together, the present study shows that the induction of visual asymmetry at the behavioral and at the morphological level in pigeons is achieved by altering neural circuits subserving perceptual and motor processes in both hemispheres. An absence of embryonic light stimulation asymmetry results in a symmetry of function in visual discrimination tasks.

Acknowledgements

Supported by a grant from the Deutsche Forschungsgemeinschaft through the Sonderforschungsbereich NEUROVISION.

References

[1] Angaut R, Repérant J. Fine structure of the optic fiber termination layers in the pigeon optic tectum: a Golgi and electron microscope study. Neuroscience 1976;1:93–105.
[2] Diekamp B, Prior H, Güntürkün O. Lateralization of serial color reversal learning in pigeons (*Columba livia*). Animal Cogn 1999;2:187–96.
[3] du Lac S, Knudsen EI. Neural maps of head movement vector and speed in the optic tectum of the barn owl. J Neurophysiol 1990;63:131–46.
[4] Engelage J, Bischof HJ. The organization of the tectofugal pathway in birds: a comparative review. In: Zeigler HP, Bischof HJ, editors. Vision, Brain, and Behavior in Birds. Cambridge, England: MIT Press, 1993:137–58.
[5] von FL, Delius JD. Long-term retention of many visual patterns by pigeons. Ethology 1989;82:141–55.
[6] von FL, Güntürkün O. Visual memory lateralization in pigeons. Neuropsychologia 1990;28:1–7.
[7] Gaston KE, Gaston MG. Unilateral memory after binocular discrimination training: left hemisphere dominance in the chick. Brain Res 1984;303:190–3.
[8] Gellermann LW. Chance orders of alternating stimuli in visual discrimination experiments. J Gen Psychol 1933;42:206–8.
[9] Güntürkün O. Lateralization of visually controlled behavior in pigeons. Physiol Behav 1985;34:575–7.
[10] Güntürkün O. The ontogeny of visual lateralization in pigeons. German J Psychol 1993;17:276–87.
[11] Güntürkün O. Morphological asymmetries of the tectum opticum in the pigeon. Exp Brain Res 1997;116:561–6.
[12] Güntürkün O. Sensory physiology: vision. In: Whittow GC, editor. Sturkie's Avian Physiology. Orlando: Academic Press, 2000:1–19.
[13] Güntürkün O, Böhringer PG. Reversal of visual lateralization after midbrain commissurotomy in pigeons. Brain Res 1987;408:1–5.
[14] Güntürkün O, Hahmann U. Functional subdivisions of the ascending visual pathways in the pigeon. Behav Brain Res 1999;98:193–201.
[15] Güntürkün O, Hellmann B, Melsbach G, Prior H. Asymmetries of representation in the visual system of pigeons. Neuroreport 1998;9:4127–30.
[16] Güntürkün O, Hoferichter HH. Neglect after section of a left telencephalotectal tract in the pigeon. Behav Brain Res 1985;18:1–9.
[17] Güntürkün O, Kesch S. Visual lateralization during feeding in pigeons. Behav Neurosci 1987;101:433–5.
[18] Güntürkün O, Kischkel KF. Is visual lateralization sex-dependent in pigeons? Behav Brain Res 1992;47:83–7.
[19] Hellmann B, Güntürkün O. The structural organization of parallel information processing within the tectofugal visual system of the pigeon. J Comp Neurol 2001;429:94–112.
[20] Hellmann B, Güntürkün O. Separate architectures for ascending and descending tectal projections in pigeons (submitted).
[21] Johnston AN, Rogers LJ. Right hemisphere involvement in imprinting memory revealed by glutamate treatment. Pharmacol Biochem Behav 1998;60:863–71.
[22] Johnston AN, Rogers LJ. Light exposure of chick embryo influences lateralized recall of imprinting memory. Behav Neurosci 1999;113:1267–73.
[23] Johnston AN, Rogers LJ, Dodd PR. [3H]MK-801 binding asymmetry in the IMHV region of dark-reared chicks is reversed by imprinting. Brain Res Bull 1995;37:5–8.
[24] Keysers C, Diekamp B, Güntürkün O. Evidence for asymmetries in the phasic intertectal interactions in the pigeon (*Columba livia*)

and their potential role in brain lateralisation. Brain Res 2000;852:406–13.
[25] Kuo ZY. Ontogeny of embryonic behavior in Aves. III. The structural and environmental factors in embryonic behavior. J Comp Psychol 1932;13:245–71.
[26] Manns M, Güntürkün O. Natural' and artificial monocular deprivation effects on thalamic soma sizes in pigeons. NeuroReport 1999a;10:3223–8.
[27] Manns M, Güntürkün O. Monocular deprivation alters the direction of functional and morphological asymmetries in the pigeon's visual system. Behav Neurosci 1999b;113:1–10.
[28] Manns M, Güntürkün O. Development and asymmetry pattern of inhibitory systems in the pigeon's visual midbrain (submitted).
[29] Mascetti GG, Vallortigara G. Why do birds sleep with one eye open? Light exposure of the chick embryo as a determinant of monocular sleep. Curr Biol 2001;11:971–4.
[30] Masino T, Knudsen EI. Anatomical pathways from the optic tectum to the spinal cord subserving orienting movements in the barn owl. Exp Brain Res 1992;92:194–208.
[31] Mench JA, Andrew RJ. Lateralization of a food search task in the domestic chick. Behav Neural Biol 1986;46:107–14.
[32] Rashid N, Andrew RJ. Right hemisphere advantage for topographic orientation in the domestic chick. Neuropsychologia 1989;27:937–48.
[33] Rogers LJ. Light experience and asymmetry of brain function in chicken. Nature 1982;297:223–5.
[34] Rogers LJ. Light input and the reversal of functional lateralization in the chicken brain. Behav Brain Res 1990;38:211–21.
[35] Rogers LJ. Behavioral, structural and neurochemical asymmetries in the avian brain: a model system for studying visual development and processing. Neurosci Biobehav Rev 1996;20:487–503.
[36] Rogers LJ, Bolden SW. Light-dependent development and asymmetry of visual projections. Neurosci Lett 1991;121:63–7.
[37] Rogers LJ, Deng C. Light experience and lateralization of the two visual pathways in the chick. Behav Brain Res 1999;98:1–15.
[38] Schwabl U, Delius JD. Visual bar length discrimination threshold in the pigeon. Bird Behav 1984;5:118–21.
[39] Tellegen AJ, Karssen AM, Rietveld TM, Dubbeldam JL. A crossed projection from the optic tectum to craniocervical premotor areas in the brainstem reticular formation. An anterograde and retrograde tracing study in the mallard (*Anas platyrhynchos* L.). Eur J Morphol 1998;36:227–43.
[40] Tommasi L, Vallortigara G. Encoding of geometric and landmark information in the left and right hemispheres of the avian brain. Behav Neurosci 2001;115:602–13.
[41] Ulrich C, Prior H, Duka T, Leshchins'ka I, Valenti P, Güntürkün O, Lipp HP. Left-hemispheric superiority for visuospatial orientation in homing pigeons. Behav Brain Res 1999;104:169–78.
[42] Vallortigara G, Cozzutti C, Tommasi L, Rogers LJ. How birds use their eyes: opposite left–right specialization for the lateral and frontal visual hemifield in the domestic chick. Curr Biol 2001;11:29–33.