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Monocular Deprivation Alters the Direction of Functional and Morphological Asymmetries in the Pigeon's (*Columba livia*) Visual System

Martina Manns and Onur Güntürkün
Ruhr-Universität Bochum

One-day-old pigeons (*Columba livia*) were monocularly deprived by occluding the left or the right eye for 10 days. Up to 3 years later, degree and direction of functional and morphological asymmetries of deprived and control pigeons were analyzed. In control pigeons, the usual right-eye superiority was obtained in a visual discrimination task. In left-eye deprived pigeons, this behavioral asymmetry was strengthened, whereas the direction of lateralization was reversed in right-eye deprived birds. A morphological tectum analysis revealed that control and left-eye deprived pigeons displayed similar asymmetries, with the left-monocular deprived pigeons exhibiting more pronounced left–right differences. Tectal morphometry of right-eye deprived pigeons displayed a reversed pattern. Overall, the present study shows that a short period of posthatch monocular deprivation is sufficient to alter behavioral and morphological visual asymmetry for several years.

The visual system of birds like chicks or pigeons is lateralized with a dominance of the right eye–left hemisphere for various visual discrimination tasks (for overviews, see Güntürkün, 1997a; Rogers, 1996). This functional lateralization is accompanied by structural asymmetries in the ascending visual thalamo- and tectofugal pathways. The avian thalamofugal system projects from the retina via the contralateral nucleus geniculatus lateralis, pars dorsalis (GLd) bilaterally to the visual Wulst of the telencephalon (Güntürkün, Miceli, & Watanabe, 1993; Miceli, Marchand, Repérant, & Rio, 1990). The tectofugal pathway comprises optic nerve fibers projecting to the contralateral optic tectum, from where fibers ascend bilaterally to the thalamic nucleus rotundus, which by itself projects to the ipsilateral ectostriatum of the forebrain (Hellmann & Güntürkün, 1999; Watanabe, Ito, & Ikushima, 1985). In chicks, right eye dominance is related to a lateralization in the organization of the contralateral projection of the GLd to the visual Wulst, which is more prominent in the left than in the right GLd (Deng & Rogers, 1998; Rogers & Sink, 1988). Tectofugal asymmetries could not be revealed in chicks (Rogers & Deng, in press). On the contrary, in pigeons structural asymmetries are observed within the tectofugal system. Already at tectal level, left–right differences in cellular soma sizes are present with retinorecipient neurons of Layers 2–12 having larger somata in the left tectum, whereas Layer 13 neurons exhibit a reversed asymmetry with larger cells in the right tectal hemisphere (Güntürkün, 1997b). Layer 13 neurons project to the nucleus rotundus, and this projection is asymmetrically organized with more fibers ascending from right tectum to left rotundus than vice versa (Güntürkün, Hellmann, Melsbach, & Prior, 1998).

The development of these behavioral and morphological visual asymmetries seems to be essentially dependent on the influence of the epigenetic factor light. Because avian embryos keep their heads turned to the right so that the right eye is close to the translucent egg shell and the left eye is occluded by the body (Kuo, 1932), the right eye receives more light stimulation than the left one. Thus, the left eye underlies a kind of natural monocular deprivation. Incubation of the embryos in darkness prevents the development of visual lateralization in chicks and pigeons (Güntürkün, 1993; Rogers, 1982; Rogers & Bolden, 1991; Zappia & Rogers, 1983). Closure of the normally more light-stimulated right eye in embryonic chicken leads to a reversal of the normal lateralization pattern (Rogers, 1990; Rogers & Sink, 1988). In chicks, the sensitive period for experimental manipulation of visual lateralization ends directly after hatching (Rogers, 1990).

However, preventing prehatching light asymmetry does not abolish the development of left–right differences in other neural systems. A large number of studies suggest that the intermediate part of the hyperstriatum ventrale (IMHV), an associative forebrain structure, is part of a memory system that mediates visual imprinting processes (Horn, 1991; Rogers, 1993). Left and right IMHV are known to interact in an asymmetrical fashion in the imprinting process, and this lateralization persists also after dark incubation (Honey, Horn, Bateson, & Walpole, 1995; Nicol, Brown, & Horn, 1995; Rogers, 1996). Thus, some aspects of lateralization

Martina Manns and Onur Güntürkün, Biopsychologie, Facultät für Psychologie, Ruhr-Universität Bochum, Bochum, Germany.

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Correspondence concerning this article should be addressed to Martina Manns, AE Biopsychologie, Facultät für Psychologie, Ruhr-Universität Bochum, 44780 Bochum, Germany. Electronic mail may be sent to mannsmbo@ruhr-uni-bochum.de.

seem to exist in birds independent of epigenetic light input asymmetries.

Pigeons are altricial birds that hatch with closed eyes and an immature visual system (Bagnoli, Porciatti, Fontanesi, & Sebastiani, 1987; Bagnoli, Porciatti, Lanfranchi & Bedini, 1985; Manns & Güntürkün, 1997). Many processes of visual development that occur before hatching in chicks proceed only after hatching in pigeons. Therefore, like in altricial zebra finches and mammals, manipulation of the visual experience might induce alterations of the visual pathway even after hatching (Herrmann & Bischof, 1986a, 1986b; Rauschecker, 1991; Sherman & Spear, 1982). Indeed, early monocular deprivation has been shown to change the biochemical properties of the visual system in pigeons (Bagnoli, Burkhalter, Vischer, Henke, & Cuénod, 1982).

The aim of the present study was to examine whether the direction of behavioral and tectal asymmetries can be influenced after hatching by monocular deprivation in young pigeons. Such an influence would corroborate the important role of light for the posthatch development of visual lateralization. Because visual asymmetries last the pigeon's entire lifespan, we studied our pigeons up to 3 years after hatching to verify if minute posthatch monocular deprivations exert effects that determine for years the functional architecture of the visual system.

Method

Materials

Young pigeons (*Columba livia,* see Table 1) were monocularly deprived directly after hatching by fixing a plastic cap on the right or left eye with a skin adhesive (Karaya paste; Hollister, Libertyville, IL). After 10 days, the caps were removed and the pigeons were raised until adulthood (6–36 months). As adults, the pigeons were tested binocularly and monocularly in a grit–grain discrimination task to check the degree and direction of visual lateralization (Güntürkün & Kesch, 1987). Afterwards, the pigeons were killed and a morphometric analysis of tectal soma sizes was performed.

For monocular behavioral tests, one eye of the pigeons was occluded with an opaque cap that was screwed to a small metal headblock. This metal block was fixed to the skull as described elsewhere (Güntürkün, 1985). The pigeons were deprived of food and maintained at 80% of their normal weight throughout the experiment.

Table 1
Pigeons That Completed All Behavioral Tasks and That Were Used in Morphometric Analyses

Group	Tectal soma size	Grit–grain discrimination
Left-eye deprived	10	7
Right-eye deprived	13	12
Control	9	9

Note. Number of pigeons in two columns differs because 4 pigeons died before the onset of behavioral tests and therefore could only be used for morphological measurements.

Grit–Grain Discrimination Task

In the grit–grain discrimination task, the pigeons had to peck 30 white grains (Dari-grains) of approximately 2 × 3 mm axial lengths from a translucent trough (9 × 5 × 6 cm) filled with small, 30-gram pebbles of varying sizes (2 to 5 mm in diameter), resembling the seeds in color and shape. About 25% of the pebbles were similar in size to the grains.

The pigeons remained in their home cages and could peck at the grain–pebble mixture when the trough was inserted under a 10 × 6 cm opening in the front panel of the cage. The animals were allowed to peck the grains for 30 s before the trough was removed. During this time, the experimenter, facing the cage from a distance of about 1 m, counted the pecks. Each 30-s trial started with the pigeon's first pecking movement. Pigeons perform different types of pecking movements, from single pecks starting from an elevated position to serial pecks executed close to the substrate (Siemann & Delius, 1992). Pecks performed as single events as well as those within a series were counted one by one. The experimenter excluded search pecks in which pigeons raked through the pebble mixture sideward and backward to uncover obstructed grains (Siemann & Delius, 1992). A video analysis of pecks displayed in slow motion and a parallel counting of pecks by different experienced observers showed a reliability of greater than 95% for the pecks counted by experimenters. The number of pecks was larger than the number of grains eaten. Thus, a considerable number of pecks terminated at the substrate. It is not possible to decide whether a peck at a pebble was planned as such or was a misdirected peck for grains. Nevertheless, the quantity of remaining grit was weighed after each session to measure the number of consumed pebbles. This procedure showed that the amount of consumed grit was close to zero.

By sorting the remaining grains, we were able to calculate the number of swallowed grains. The percentage of pecks leading to consumption served as an index of discrimination accuracy. This parameter was calculated as the number of grains swallowed multiplied by 100 and divided by the number of pecks. Because of this kind of analysis, discrimination accuracy was about 60% in the present experiment.

Each pigeon completed 20 binocular sessions, with 2 sessions per day. During the first 10 sessions, the pigeons were allowed to habituate to the procedure. We included the subsequent 10 tests in the behavioral analysis. The pigeons were then tested under monocular conditions, with 20 sessions for the left and the right eyes, respectively. Again, the first 10 sessions under each eye cap condition served for habituation. However, plotting an acquisition curve over all 20 tests showed that independent of the seeing condition, the pigeons achieved a very high level of discrimination accuracy as early as the first session. This performance did not improve during the subsequent tests. Thus, our results were not influenced by learning effects. These data suggest that the grit–grain discrimination task required skills that the pigeons already possessed when testing started. It is probably a natural and well practiced behavior for adult pigeons to peck grains from a noisy substrate.

Each pigeon was tested twice a day with the right and the left eye seeing in balanced order, so that each pigeon performed four sessions every day. The experiments started alternately with the left or the right eye seeing. Pilot studies had shown that four tests per day did not influence performance.

Histology

When the behavioral tests were completed, the pigeons were anesthetized with an overdose of equitesin (0.55 ml/100 g body

weight) and perfused through the heart with 0.9% (wt/vol) saline (40 °C) followed by 4% paraformaldehyde (in 0.12 M phosphate buffer, 4 °C, pH 7.2). The brains were removed and postfixed in 4% paraformaldehyde + 30% (wt/vol) sucrose, cryoprotected in 0.12 M phosphate buffer + 30% sucrose at 4 °C for 24 hr and cryosectioned in frontal plane at 30 μm. Sections were mounted on gelatinized slides, stained with cresyl violet, and covered.

Because of the long-term nature of the study, 5 of 33 pigeons died before the behavioral experiments could be performed. In 4 of these 5 pigeons, we were able to rapidly immersionfix the brains and save them for histology without noticeable reductions in morphological quality and without alterations in morphometric results.

For tectal soma size measurements, we selected only sections corresponding to the stereotaxic level A 3.75 (Karten & Hodos, 1967). In each hemisphere, the soma size of tectal neurons in Layers 2–13 situated in the lateral portion of the tectal tangential plane was determined. Measurements were performed in Layers 2–13 (nomenclature according to Cajal, 1911, 1995), because Lamina 1, as a pure fiber layer, does not contain neurons. Layers 14–15 were excluded because Güntürkün (1997b) did not observe significant asymmetries in these laminae. The cross-sectional soma areas of 50 cells in each layer of each hemisphere were measured with the image analyzing system Analysis (SIS, Münster, Germany). A previous analysis with sample sizes of 20, 30, 50, 70, 100, 150, and 300 neurons of Lamina 13 had shown that the analysis of 50 cells suffices to yield a mean that was close to the average of 300 neurons (within 5% of the standard error). We considered only neurons containing a clear nucleolus, a round and lightly colored nucleus, and visible Nissl substance in the cytoplasm. The boundaries of these cells were drawn by tracking the image displayed on the video screen with a computer mouse. The display was obtained with a Kappa CF8 camera (Gleichen, Germany) attached to an Olympus BH-2 microscope (Olympus Europe, Hamburg, Germany) with a 100× objective. The image-analyzing system calculated the surface encircled. After the image was centered on a certain layer, each cell within the boundaries of the monitor screen was measured. After all neurons were analyzed the microscope stage was moved slightly to view the directly adjacent portion of the tectal section. Because this morphometric analysis was performed in 32 preparates (see Table 1), a total of 38,400 tectal neurons (32 animals × 2 hemispheres × 12 layers × 50 cells) were measured.

Statistical Analysis

Statistical analysis of the data was performed with the help of the PC-based statistic programs Statistica (StatSoft, Tulsa, OK) and SPSS (SPSS, Munich, Germany). We compared left–right differences within and between the three groups by using a multivariate analysis of variance for repeated measures (MANOVA). In case of a significant result of an overall analysis, we used paired *t* tests and Tukey's honestly significant difference (HSD) tests for single comparisons. Planned comparisons were performed by orthogonal contrasts and group differences in the extent of asymmetries were evaluated with an analysis of variance (ANOVA).

Results

Grit–Grain Discrimination

To compare the performances of the three groups, we performed a two-factorial (Group × Seeing Condition) MANOVA. This analysis revealed no significant main effect of group, $F(1, 27) = 1.57, p = .226$, but a significant seeing condition effect, $F(2, 54) = 45.98, p < .001$. In addition, both factors evinced a highly significant interaction, $F(4, 54) = 6.13, p < .001$.

All groups achieved their best discrimination results under binocular seeing conditions (see Figure 1). An orthogonal contrast comparing binocular performances with monocular ones in all groups confirmed the significance of this difference, $F(1, 27) = 98.59, p < .001$. Furthermore, as outlined below, all groups exhibited left–right differences in their discrimination accuracies (see Figure 1). According to an orthogonal contrast between performances of left and right eye seeing conditions in all pigeons, this difference was significant, $F(1, 27) = 9.70, p < .01$. Control and left-eye deprived pigeons achieved higher discrimination accuracies seeing with their right eyes ($p < .05$ for each paired sample *t* test; see Figure 1A and B). On the contrary, right-eye-deprived pigeons achieved a significantly better discrimination accuracy seeing with their left eye (paired sample *t* test $p < .05$; see Figure 1C). Because these differences between the eye conditions resulted from a higher number of consumed grains and not from the number of performed pecks (Figure 2), monocular deprivation seemed to influence visual discrimination without altering pecking performance in the present task.

To compare left–right differences in discrimination performance between groups, a lateralization index (LI) for the extent of functional asymmetry was estimated. This was calculated as:

$$\mathrm{LI} = \frac{\text{discrimination accuracy right eye} - \text{discrimination accuracy left eye}}{\text{discrimination accuracy right eye} + \text{discrimination accuracy left eye}}. \quad (1)$$

Positive LI values indicate a right-eye advantage whereas a left-eye superiority results in negative values (see Figure 1, panel D). A one-way ANOVA revealed a significant group effect in the extent of LI, $F(2, 27) = 7.17, p < .01$. Orthogonal contrasts demonstrated that the opposing direction in LI magnitude between right-eye-deprived pigeons and the other two groups was significant, $F(1, 27) = 10.50, p < .01$. In addition, the right-eye advantage was significantly increased in left-eye-deprived pigeons compared with both other groups, orthogonal contrasts $F(1, 27) = 10.69, p < .01$ (see Figure 1D). A post hoc comparison (Tukey's HSD test) demonstrated that only left- and right-eye-deprived groups differed significantly from each other ($p < .01$), whereas control pigeons held a middle position in the extent of their functional asymmetry. Overall, these analyses revealed a strong influence of monocular deprivation on discrimination accuracy, with an increase of the usual right-eye advantage in left-eye-deprived pigeons and a reversal of lateralization in right-eye-deprived pigeons (see Figure 1).

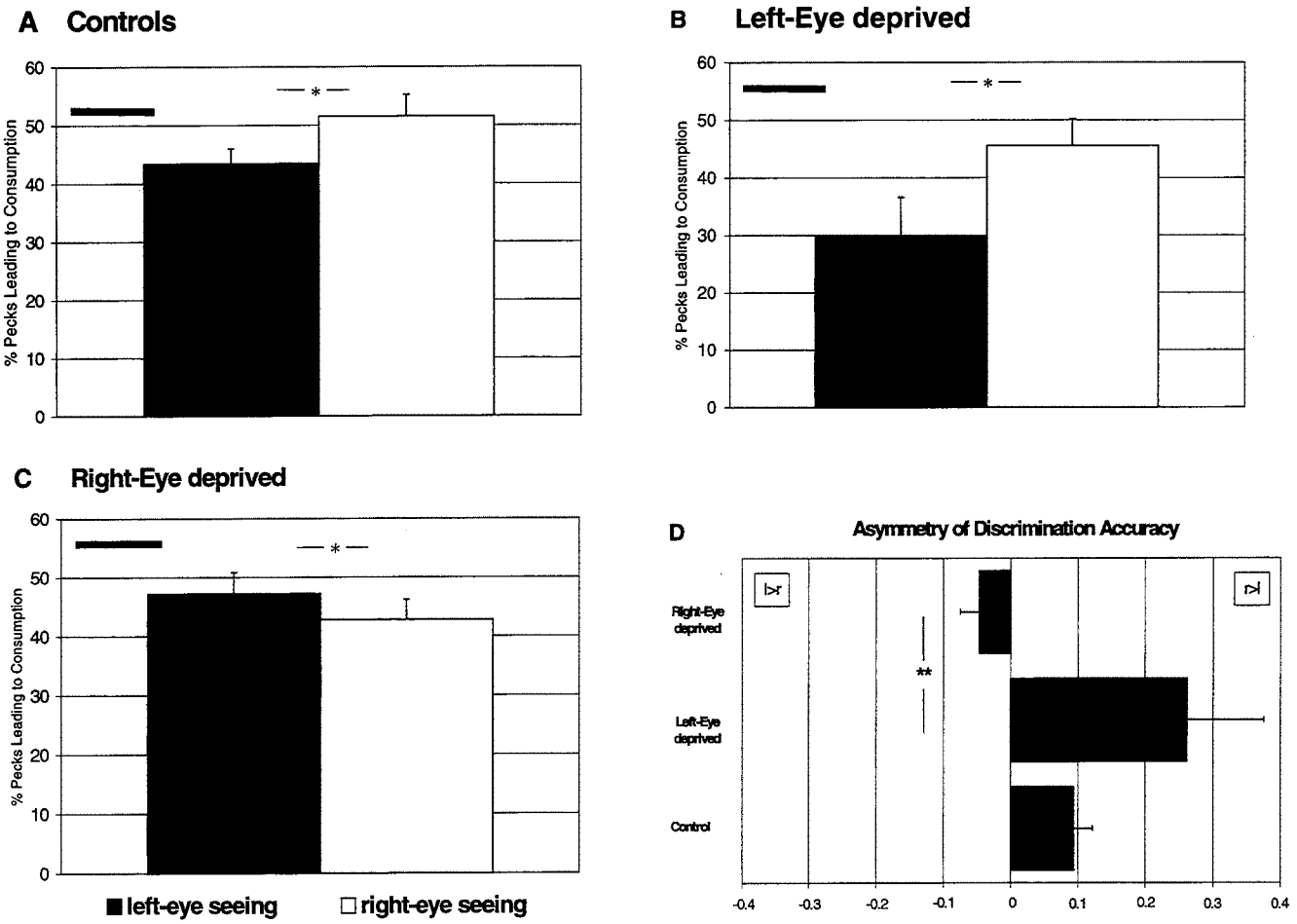


Figure 1. Left- and right-eye seeing discrimination performance of the three groups in the grit–grain discrimination task. Solid horizontal lines indicate binocular performance. A: control pigeons; B: left-eye-deprived pigeons; C: right-eye-deprived pigeons; D: percentage of asymmetry in discrimination accuracy. Negative values indicate a left-eye advantage (l > r); positive values indicate a right-eye advantage (r > l). Bars represent standard errors, which were calculated by using the number of pigeons as the relevant value for *n*. $*p < .05$ and $**p < .01$, according to post hoc comparisons.

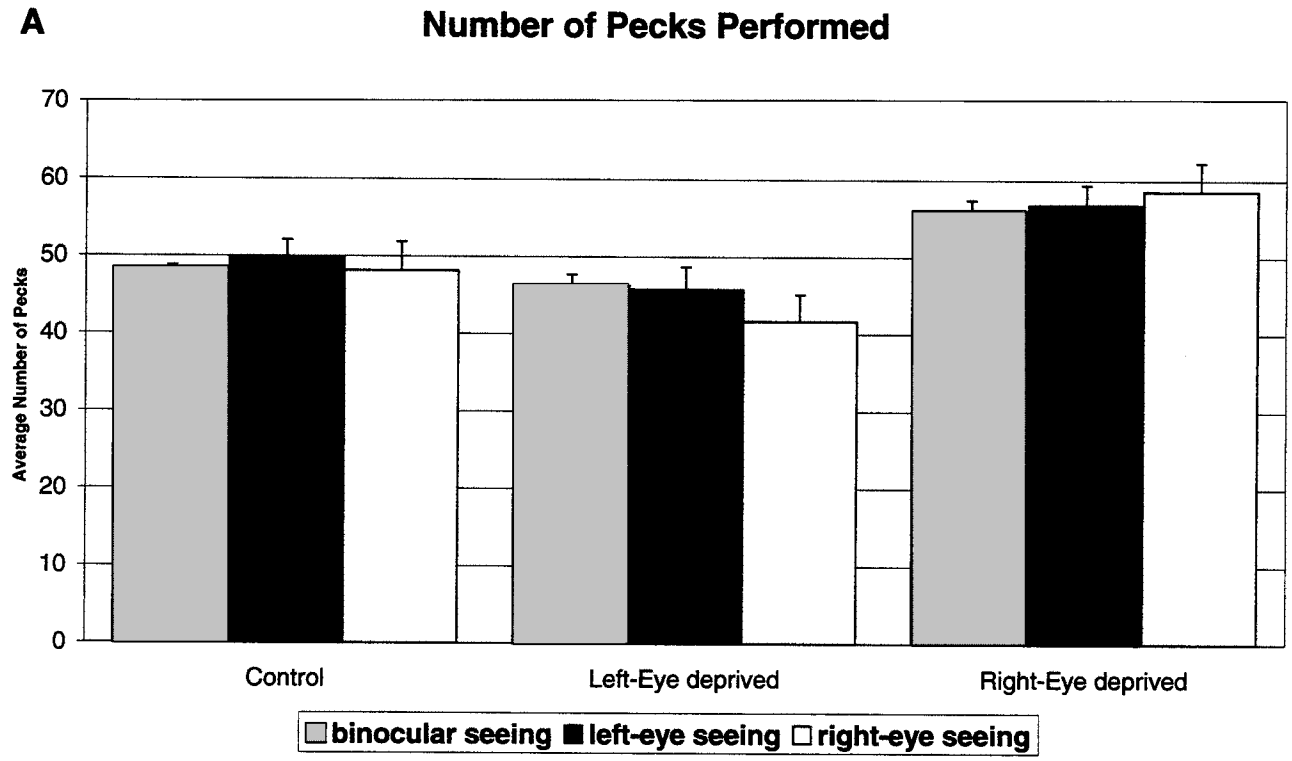
Tectal Soma Size

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

1. Layers 2–7 were grouped as those retinorecipient layers where retinal fibers terminate (Angaut & Repérant, 1976; Repérant & Angaut, 1977).
2. Layers 8–12 were grouped as those retinoreceptive layers that receive direct retinal input by ascending dendrites without projecting to the nucleus rotundus (Bagnoli, Francesconi, & Magni, 1979; Hardy, Leresche, & Jassik-Gerschenfeld, 1985).
3. Layer 13 was analyzed separately because it constitutes the projection lamina to the rotundus (Hellmann & Güntürkün, 1999).

We analyzed left–right differences in tectal soma size between groups by performing a three-factorial (Group × Hemisphere × Layer) MANOVA. This analysis revealed a significant influence of the layer variable, $F(2, 56) = 294.10$, $p < .001$, but not of the variables group, $F(2, 28) = 1.67$, $p = .207$, or hemisphere, $F(1, 28) = 2.20$, $p = .15$. Whereas Group × Layer, $F(4, 56) = 7.84$, $p < .001$, and Hemisphere × Layer, $F(2, 56) = 5.32$, $p < .01$, interactions were significant, the Group × Hemisphere interaction was not, $F(2, 28) = 1.71$, $p = .2$. In addition, there was a significant Group × Hemisphere × Layer interaction, $F(4, 56) = 3.31$, $p < .05$.

In control and left-eye-deprived pigeons, retinorecipient Layers 2–12 exhibited larger somata within the left tectum. According to an orthogonal contrast, this difference approached significance, $F(1, 28) = 3.17$, $p = .086$. However, whereas in controls this asymmetry pattern was especially pronounced in deeper Layers 8–12, in left-eye-deprived



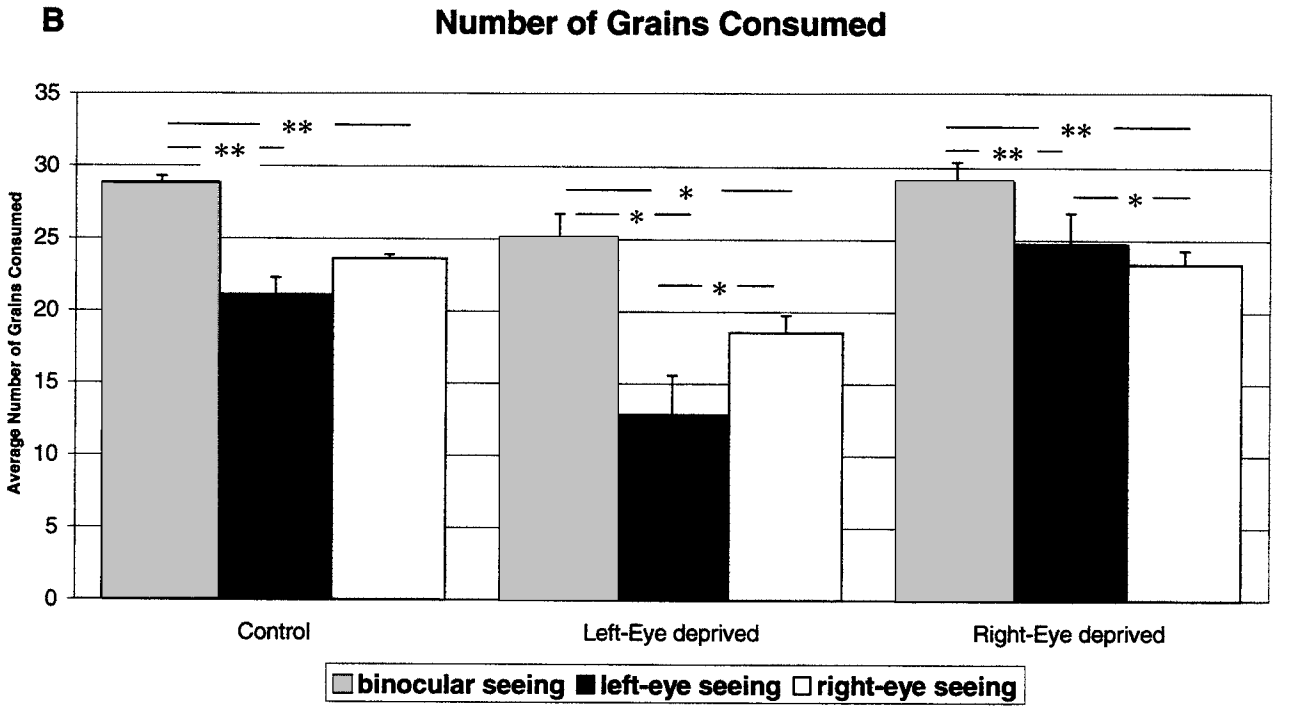


Figure 2. A: Number of performed pecks in the grit–grain discrimination task; B: Number of grains swallowed. $*p < .05$ and $**p < .01$, according to paired-sample t tests.

pigeons the left-skewed asymmetry of the retinorecipient layers was slightly more prominent in the superficial Laminae 2–7 (see Figure 3A, B, and D). Compared with this, the projection Layer 13 showed a reversed soma size asymmetry with larger neurons in the right tectum (see Figure 3A, B, and D). An orthogonal contrast confirmed the significance of these left–right differences, $F(1, 28) = 6.03$, $p < .05$. However, a post hoc comparison showed that only left–right differences in Layer 13 soma sizes of the left-eye-deprived pigeons achieved significance (Tukey's HSD, $p < .05$). The morphological asymmetry data for controls confirmed earlier results (Güntürkün, 1997b), whereas the results obtained in left-eye-deprived pigeons seemed to reflect an increase of this pattern at least for Layers 2–7 and Lamina 13.

In right-eye-deprived pigeons, the asymmetry pattern was reversed compared with the other groups. Contrary to the pattern described in the other pigeons, retinorecipient layers displayed a right-skewed asymmetry that was especially pronounced in superficial Layers 2–7. Lamina 13 had a small bias to have larger somata on the left (see Figure 3C and D).

To better compare tectal asymmetries between the groups, we calculated the extent of tectal soma size asymmetry (TA) as the percentage deviation from mean soma size:

$$\mathrm{TA} = \frac{\text{Mean soma size of left and right tectum} - \text{Soma size left tectum} \times 100}{\text{Mean soma size of left and right tectum}}. \quad (2)$$

Positive values indicate larger somata in right tectum, whereas larger cells in left tectum result in negative values (Figure 3).

A two-way (Experimental Group × Layer) ANOVA with TA values revealed a significant main effect for layer, $F(2, 56) = 4.10$, $p < .05$, but not for group, $F(2, 56) = 0.22$, $p = .804$. The interaction between these variables was significant, $F(4, 56) = 4.16$, $p < .01$. Orthogonal contrasts among right-eye- and left-eye-deprived and control pigeons showed that soma size asymmetries of superficial Layers 2–7 approached significance, $F(1, 28) = 3.85$, $p = .059$ (Figure 3D). The asymmetry of Layer 13 neurons was virtually absent in right-eye-deprived pigeons, but pronounced in the other two groups. Consequently, orthogonal contrasts revealed a significant difference in this group comparison, $F(1, 28) = 4.32$, $p < .05$.

Discussion

The present data clearly show that the direction of the functional and the morphological lateralization of the pigeon's visual system can be still influenced after hatching by manipulating visual experience. These results confirm the important role of light as an epigenetic factor for the development of visual asymmetries. Deprivation of the normally dominant right eye resulted in a reversal of behavioral and structural asymmetries whereas deprivation of the left eye strengthened right-eye dominance. This shows that the asymmetries induced before hatch can be modified by short posthatch environmental influences and are stabilized in the subsequent development of visual circuits that last a pigeon's entire life.

Deprivation Effects

In the grit–grain discrimination task, all groups revealed significant differences in their monocular performances. Because left- and right-eye-deprived pigeons achieved reduced scores with their deprived eye, differences in their discrimination performance might have resulted from deprivation-induced optic damages. This seems unlikely because aberrations of the optic apparatus were not observed even after long-term deprivations of up to 257 days (Burkhalter & Cuénod, 1978). Therefore, the alteration of behavioral visual asymmetry in adult pigeons several years after a rather brief posthatch monocular deprivation is very likely due to changes of central mechanisms. This accords with our anatomical observations that the pigeon's tectum undergoes important developmental changes within the first 2 posthatch weeks (Manns & Güntürkün, 1997).

The modifications of the lateralization pattern observed in the present study suggest that the embryologically induced lateralization pattern has to be stabilized during posthatch maturation of visual circuits. This implies that asymmetries induced before hatch have to be consolidated under conditions of a symmetrical light input. At present it is only possible to speculate about the mechanisms involved in this process. Embryologically intended asymmetries are sufficient to induce posthatch imbalances between the hemispheres. It is conceivable that these imbalances could be mediated by asymmetries of interhemispheric interactions that might constitute negative feedback loops and thereby stabilize initial left–right differences. Indeed, the tectotectal interaction is mainly inhibitory (Hardy, Leresch, & Jassick-Gerschenfeld, 1984; Robert & Cuénod, 1969), is possibly asymmetrically organized (Keysers, Diekamp, & Güntürkün, 1998), and the transsection of the tectal and the posterior commissures results in a reversal of visual lateralization (Güntürkün & Böhringer, 1987). Thus, posthatch asymmetries of tectotectal interaction may replace the prehatch asymmetry of light input to consolidate visual lateralization during a critical period of plasticity.

This developmental course contrasts with the pattern observed in the precocial domestic chick. Its visual pathways mature at a much faster rate, so similar reversals of asymmetry occur only after covering the right eye of the embryo within the egg and exposing the left eye to light (Rogers, 1990; Rogers & Sink, 1988). Thus, embryonic light affects the visual systems of chicks and pigeons at different developmental stages characterized by different capacities for plasticity. Whereas in chicks prehatch light influences a rather developed system (for a review, see Mey & Thanos, 1992), in the pigeon, light exerts asymmetrical influences on a visual system that is far less functional (Bagnoli et al., 1985, 1987) and is still modifiable after hatching. These differences in developmental speed might be related to the differences in anatomical asymmetries observed between pigeons and chicks. Whereas in pigeons the tectorotundal

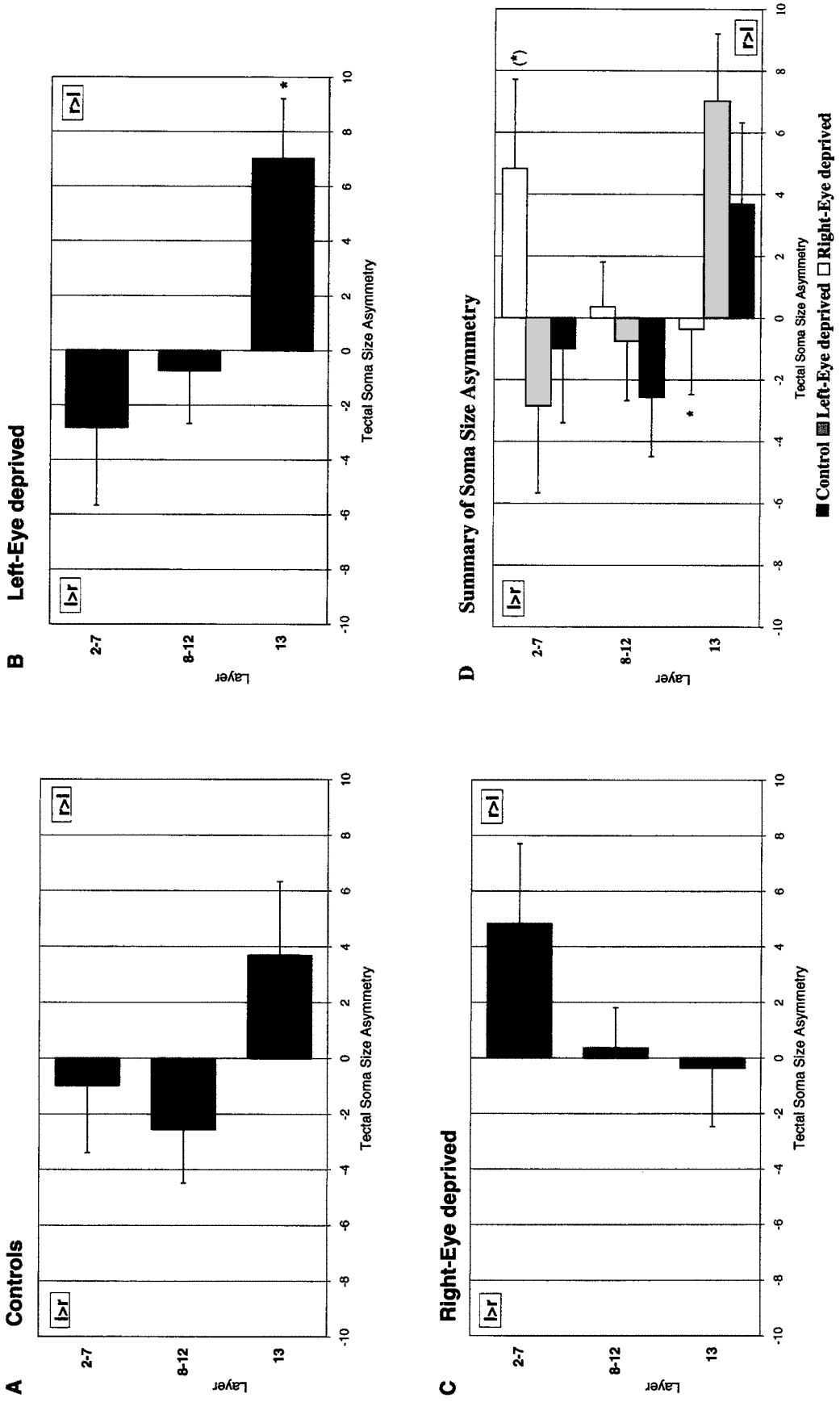


Figure 3. Tectal soma size asymmetries in different layer groupings (Laminae 2–7, Laminae 8–12, Lamina 13) depicted as the percentage size difference between left and right tectal hemisphere. Negative values indicate larger neurons on the left side (1 > r); positive values indicate larger cells on the right side (r > 1). A: control pigeons; B: left-eye deprived pigeons; C: right-eye deprived pigeons; D: comparison of tectal asymmetry (TA) values in different layers between the three groups of pigeons. Bars indicate standard errors of the TA values. (*)$p = .059$, *$p < .05$, according to post hoc comparisons.

projection is asymmetrically organized (Güntürkün et al., 1998), in chicks tectofugal asymmetries are absent and thalamofugal left–right differences predominate (Rogers & Deng, in press).

Tectal Soma Size Asymmetry

Monocular deprivation also influences the pattern of soma size asymmetry in the optic tectum. Overall, the analysis of the morphological data revealed that control and left-eye-deprived pigeons displayed very similar results, with the left-monocular-deprived pigeons exhibiting more pronounced left–right differences. Because the natural prehatching condition of pigeons resembles a natural monocular deprivation of the left eye, the results of the left-eye-deprived pigeons are a mere increase of the very same effect. The tectal morphology pattern of the right-eye-deprived pigeons, on the other hand, displayed a reversal of the pattern observed in the other two groups. This reversal was especially pronounced in the superficial retinorecipient Layers 2–7. This pattern probably reflects the developmental tectal gradient from the deepest to the superficial tectal layers (Domesick & Morest, 1977; LaVail & Cowan, 1971). The retinorecipient Layers 2–7 are those that are not fully constituted after hatching and bear many migrating and undifferentiated cells that only start to establish their synaptic connections (Manns & Güntürkün, 1997). Thus, the superficial tectal neurons might possess the largest potential for morphological alterations.

These neuronal changes are probably induced by activity-dependent influences on tectal neurons. Because of the asymmetric photic stimulation of both eyes, activity-dependent processes could lead to a lateralized release of neurotrophic factors and thus to an asymmetric alteration of tectal cell morphologies, cellular activities, or both (Güntürkün, 1997b, 1997c). These processes could determine the emergence of asymmetrical visual circuits constituting functional left–right differences. These embryonic tectal asymmetries have to be stabilized during the posthatch development and thus remain modifiable by environmental influences during a critical window of time. Posthatch monocular deprivation probably acts along the same principles by altering retinotectal activity patterns, leading to changes of the asymmetries that were established before hatch.

However, this model cannot directly explain the soma size asymmetry of Layer 13 neurons (Güntürkün, 1997b). An indirect mechanism must explain an asymmetry pattern with larger cells in the less activated hemisphere. This finding closely resembles a paradoxical effect in the mammalian visual cortex: infusion of brain derived neutrotrophic factor (BDNF) into the visual cortex of monocularly deprived kittens reverses monocular deprivation effects so that a high number of cortical cells respond to the deprived eye (Galuske, Kim, Castrén, & Singer, 1994). Very similar results were achieved by the infusion of the GABA agonist muscimol (Reiter & Stryker, 1988). Because GABAergic cortical cells express high amounts of BDNF-binding tyrosine kinase B receptors (Widmer & Hefti, 1994) this paradoxical effect might result from a selective activation of these inhibitory neurons (Bonhoeffer, 1996). A similar mechanism might explain the reversed asymmetry of Layer 13 soma size. A subpopulation of Layer 13 neurons are known to obtain direct retinal input by ascending dendrites reaching up to Layers 4 and 5 (Hellmann & Güntürkün, 1999; Karten, Cox, & Mpodozis, 1997; Luksch, Cox, & Karten, 1998). These cells are also radially connected with interneurons from the superficial retinorecipient laminae (Hardy et al., 1985). Hunt and Künzle (1976) demonstrated the existence of GABAergic tectal interneurons, whereas Bagnoli, Francesconi, and Magni (1977) demonstrated in an electrophysiological study inhibitory intratectal neurons, which project onto Layer 13 neurons. Thus, the stronger activation of these GABAergic tectal interneurons might cause a stronger suppression of activity of Layer 13 neurons in the left tectum, resulting in smaller neurons in the dominant hemisphere. Left-eye deprivation could strengthen this effect whereas right-eye deprivation levels the intended asymmetries, thereby abolishing left–right differences in the soma size of Layer 13 neurons.

Relationship Between Tectal and Functional Asymmetries

Morphological asymmetries of the tectum might constitute the basis for lateralized visual circuits within the tectofugal system. Indeed, both behavioral and tectal asymmetries are influenced by light input. Consequently, we found a reversal of functional lateralization in right-eye-deprived pigeons that was associated with deviations of tectal soma size asymmetry. However, this deviated lateralization pattern did not simply mirror the pattern observed in controls. Instead, the usual pattern of tectal cell size asymmetries with a left-skew of Layers 2–12 and a right-skew of Layer 13 was almost completely reduced to a right-skew of the superficial Layers 2–7 in right-eye-deprived pigeons. Behaviorally, these birds exhibited a clear left-eye dominance. Thus, different intratectal or tectofugal neural wiring patterns might be able to induce a functional visual lateralization. This opens the possibility that different neural solutions could result in similar behavioral asymmetries.

The results of the present study suggest that the interplay of embryonic and posthatch visual experience determines the direction and degree of visual lateralization in pigeons. During a short, critical time, minute imbalances of visual input are sufficient to influence the formation of asymmetrical neuronal features with lifelong effects on lateralized visual performance. The important trigger function of an asymmetrical light input indicates that the formation of lateralized visual properties is mediated by activity-driven processes. It is therefore conceivable that the processes involved are similar to the events that determine the maturation of the mammalian visual system (for reviews, see Cellerino & Maffei, 1996; Rauschecker, 1991). It is an exciting prospect that the emergence of cerebral asymmetries, which still are an enigma in so many lateralized systems, might develop along rules already known in developmental neurobiology.

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