

Lateralized Interhemispheric Transfer of Color Cues: Evidence for Dynamic Coding Principles of Visual Lateralization in Pigeons

Martina Skiba, Bettina Diekamp, Helmut Prior, and Onur Güntürkün

AE Biopsychologie, Fakultät für Psychologie, Ruhr-Universität Bochum, Bochum, Germany

Visual feature discrimination tasks in pigeons reveal a right eye/left hemisphere dominance at the population level. Anatomical studies and lesion data show this visual lateralization to be related to asymmetries of the tectofugal system, which ascends from the tectum over the *n. rotundus* to the forebrain. Anatomically, this system is characterized by numerous morphological and connectional asymmetries which result in a bilateral visual representation in the dominant left hemisphere and a mostly contralateral representation in the subdominant right hemisphere. Ontogenetically, visual lateralization starts with an asymmetrical embryonic position within the egg, which leads to asymmetries of light stimulation. Differences in exposure to light stimulation between the eyes result in activity differences between the ascending tectofugal pathways of the left and the right hemisphere, which are transcribed during a critical time span into morphological asymmetries. The asymmetries established after this transient period finally start to determine the lateralized processes of the visual system for the entire life span of the individual. We now can show that these anatomical lateralizations are accompanied by asymmetries of interocular transfer, which enable a faster shift of learned color cues from the dominant right to the left eye than vice versa. In summary, our data provide evidence that cerebral asymmetries are based both on “static” anatomical and on “dynamic” process-dependent principles. © 2000 Academic Press

Key Words: cerebral asymmetry; tectofugal system; *n. rotundus*; interocular transfer; birds.

INTRODUCTION

Before embarking into deeper considerations, some sobering prolegomena seem to be in place. We have known for about 135 years (Broca, 1865) that our brain is asymmetrically organized. In this span of time scientists have discovered countless lateralized sensory, cognitive, emotional, or motor

Address correspondence and reprint requests to Onur Güntürkün, AE Biopsychologie, Fakultät für Psychologie, Ruhr-Universität Bochum, 44780 Bochum, Germany. Fax: + 49–234–32 14377. E-mail: onur.guentuerkuen@ruhr-uni-bochum.de.

functions as well as several dozen neural systems which display anatomical left–right differences (Davidson & Hugdahl, 1995; Hellige, 1993). Despite these discoveries, which seem to reflect a true scientific success story, we have progressed little in lateralization research. We still do not know how ontogenetic variables shape the primordial brain into asymmetry. Likewise, we have few clues as to how asymmetries of anatomy are translated into the lateralized functioning of a whole brain, with all its interhemispheric interactions.

Some of the limitations of our knowledge are due to the fact that the vast majority of asymmetry studies are performed in humans. A deeper experimental analysis of the ontogenetic scenario and the neural architecture which governs lateralized behavior is therefore limited. Although animal studies which are free of these restrictions gained momentum in the past 2 decades, the majority of neuropsychologists are still not fully aware of the explanatory potential of these approaches. In the present article we therefore review some of the studies on visual lateralization in pigeons and present an experiment which demonstrates that interhemispheric interactions subsequent to visual learning are asymmetrically organized. Numerous studies on visual asymmetry have also been pursued in other birds like the domestic chick. Since experiments on laterality in birds covering a wide range of species have been reviewed recently (Rogers, 1996; Güntürkün, 1997a), we do not extensively discuss these other avian asymmetry models.

VISUAL LATERALIZATION IN PIGEONS: BEHAVIORAL ANALYSIS

The optic nerves of birds cross completely at the optic chiasm and only small amounts of fibers recross in the midbrain and thalamic commissures (Weidner et al., 1985). Thus, the performance of one halfbrain can easily be studied using eyecaps with which sight can temporarily be restricted to one eye, thus directing the information to the contralateral hemisphere. With this procedure, visual lateralization can be demonstrated using a wide range of techniques. In pigeons, the right eye system is superior in discriminating two-dimensional artificial patterns (Güntürkün, 1985) and three-dimensional natural objects (Güntürkün & Kesch, 1987).

Moreover, some of the neural processes leading to the perception of a geometrical optic illusion are lateralized (Güntürkün, 1997b). The greater visual processing capacity of the right eye/left hemisphere for pattern discrimination makes the dominant side more susceptible to the herringbone illusion. In visual memory tasks in which 725 abstract patterns have to be memorized, the animals are able to remember most of them with their right eye, but are barely above chance level with their left (von Fersen & Güntürkün, 1990). It is probably this asymmetry in memorizing visual stimuli which results in a significant right-eye advantage when homing from a release site over known territory to the loft (Ulrich et al., 1999). The visual lateralization

also affects cognitive processes of the animals such that visual "learning-to-learn" effects develop faster and with a higher performance using the right eye (Diekamp et al., 1999). Due to the complete decussation of the optic nerve, this right-eye superiority is probably related to a left hemisphere dominance for visual object analysis. This assumption is supported by the fact that lateralized performance is not caused by peripheral factors such as differences in visual acuity, wavelength discrimination, or depth resolution (Martinoya et al., 1988; Remy & Emmerton, 1991; Güntürkün & Hahmann, 1994). A further argument for left cerebral dominance includes behavioral results which show that unilateral left-hemisphere lesions attenuate visual discrimination performance or cause severe deficits of visual acuity, while right-sided lesions have minor impact (Güntürkün & Hoferichter, 1985; Güntürkün & Hahmann, 1999). This left-hemisphere superiority for visual object analysis is not restricted to pigeons but has been also described with various methods in domestic chicks (Mench & Andrew, 1986; Vallortigara et al., 1996; Rogers, 1996), zebra finches (Alonso, 1998), and food-storing and nonstoring parids and corvids (Clayton & Krebs, 1994).

VISUAL LATERALIZATION IN PIGEONS: ANATOMICAL FOUNDATIONS

In birds, visual information ascending to the forebrain is processed by two parallel pathways, the thalamofugal and the tectofugal system, suggested to be equivalent to the geniculocortical and the extrageniculocortical visual pathways of mammals, respectively (Shimizu & Karten, 1993). The pigeon's thalamofugal pathway mainly processes visual input from the lateral monocular fields of the laterally placed eyes (Remy & Güntürkün, 1991; Güntürkün & Hahmann, 1999). In the asymmetry experiments with pigeons reviewed up to now, however, the stimuli were viewed by the frontal binocular visual field, which is mainly analyzed by the tectofugal pathway (Hellmann & Güntürkün, 1999; Güntürkün & Hahmann, 1999). The tectofugal system is composed of optic nerve fibers projecting to the contralateral optic tectum, from which fibers lead bilaterally to the thalamic n. rotundus, which itself projects to the ipsilateral ectostriatum of the forebrain (Engelage & Bischof, 1993) (Fig. 1). In chicks, the thalamofugal system is asymmetrically organized with more contralateral visual projections of the left nucleus geniculatus lateralis, pars dorsalis (GLd), to the right hyperstriatum than vice versa (Rogers, 1996). This structural disproportionateness has shown to be related to lateralized visual behavior, such as categorization of stimuli or passive-avoidance learning.

In pigeons, the tectofugal system shows morphological asymmetries. In the tectum the size of perikarya of superficially located retinorecipient cells have found to be larger on the left side, contralateral to the dominant eye (Fig. 1, box 1) (Güntürkün, 1997c). This is also the case for the n. rotundus,

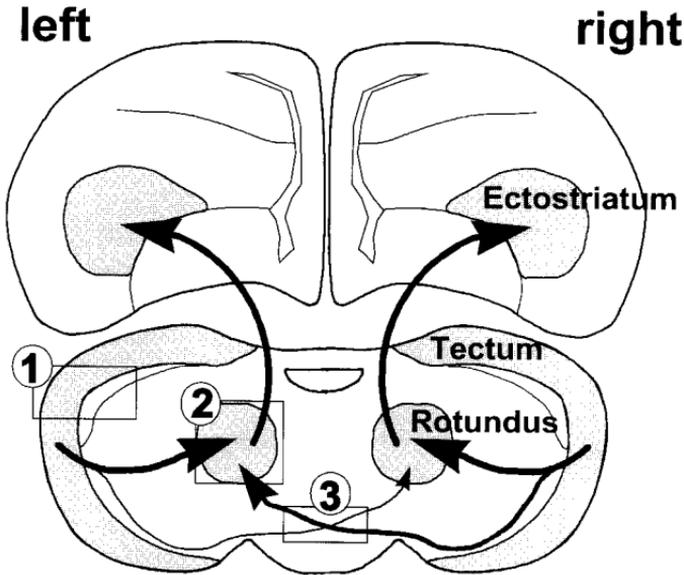


FIG. 1. Schematic overview of the pigeons' tectofugal system. The lower part represents a frontal section at the midbrain/thalamus junction, while the upper part depicts a section of the forebrain. The tectum of the midbrain, the thalamic n. rotundus, and the forebrain ectostriatum are shown in gray. Boxes with numbers denominate the three tectofugal components for which anatomical asymmetries have been shown: (1) morphological soma size asymmetries in the superficial retinorecipient and the deep relay neurons of the tectum (Güntürkün, 1997c); (2) morphological soma size asymmetries of relay neurons in the n. rotundus (Manns & Güntürkün, 1999b); (3) connectional asymmetries with significantly more axons projecting from right tectum to left rotundus than from left tectum to right rotundus, resulting in an increased bilateral representation on the left side (Güntürkün et al., 1998).

the next tectofugal entity (Fig. 1, box 2) (Manns & Güntürkün, 1999b). Thus, the pigeon's tectofugal system displays significant morphological asymmetries which might be related to the behavioral lateralization of the animals.

Relay neurons of the tectal lamina 13 project bilaterally onto the n. rotundus (Hellmann & Güntürkün, 1999). The bilaterality of this projection should lead to representations of both the ipsi- and the contralateral eye in the tectofugal system of each hemisphere. Indeed, Engelage and Bischof (1988) showed binocular input to be represented in the tectofugal pathway in zebra finches. In pigeons, Güntürkün et al. (1998) demonstrated with anterograde and retrograde tracers that the ratio of ipsi- to contralateral tectorotundal projections is asymmetrical (Fig. 1, box 1). While the quantity of ipsilateral tectorotundal projections is about equal, the number of neurons projecting contralaterally from the right tectum to the left rotundus are about twice in number than vice versa. As a result, the n. rotundus on the dominant left side receives, besides a massive ipsilateral tectal input, also a large number of afferents from the contralateral tectum. Consequently, the visual input

of the n. rotundus of the dominant left hemisphere is to a significantly higher degree bilaterally organized than its counterpart in the right halfbrain. Functionally, this anatomical condition could enable the left rotundus to integrate and process visual inputs from both eyes and thus from both sides of the visual world. Indeed, a recent lesion study showed that processes of the left rotundus are significantly related to acuity performance with the right and the left eye, while the right rotundus only had minor relevance (Güntürkün & Hahmann, 1999).

THE ONTOGENY OF VISUAL LATERALIZATION IN PIGEONS

The development of structural and functional asymmetries in birds is triggered by the epigenetic factor of light. Avian embryos lie within the egg so placed that their right eye is close to the translucent eggshell while the left eye is occluded by its own body (Kuo, 1932). This asymmetric position results in stronger light stimulation of the right eye during embryogenesis. In pigeons this "natural monocular deprivation" of the left eye triggers the functional establishment of visual lateralization with right-eye superiority, which becomes obvious in different behavioral tasks, such as categorizing food from nonfood or distinguishing between abstract stimuli (Manns & Güntürkün 1999a, Güntürkün, 1993). In chicks and pigeons, dark incubation before hatch prevents the establishment of visual asymmetries (Rogers, 1982; Güntürkün, 1993). In pigeons, posthatch monocular deprivation of the right eye for 10 days reverses asymmetry, while the same treatment of the left eye enhances the usual right-eye dominance (Manns & Güntürkün, 1999a). Visual lateralization is not altered if 20-day-old pigeons are monocularly light deprived for 10 days (Manns, 1998). Thus, manipulations of visual experience can modify functional asymmetries during a sensitive time frame. This window is extended into the posthatching period in pigeons but is confined to the embryonic phase in chicks (Rogers, 1982, 1990).

Manipulations of visual experience during a critical time span directly after hatching not only alter behavioral left-right differences, but concomitantly also change anatomical asymmetries of the ascending visual pathways. The usual left-skewed asymmetry of retinorecipient tectal neurons is enhanced after left-eye deprivation and abolished after right-eye closure (Manns & Güntürkün, 1999a). These data make it likely that light stimulation acts in an activity-dependent manner to induce structural asymmetries in the pigeon's tectofugal pathway. Thus, at first glance, these results might point to close similarities of the mechanisms which govern the ontogeny of visual asymmetry in birds and the geniculocortical effects of monocular deprivation in mammals. However, although seemingly similar, different mechanisms might be involved.

Morphological soma size effects of monocular deprivation in mammals are restricted to the binocular portion of the lateral geniculate nucleus and

are absent in the retina and the visual cortex (Sherman & Spear, 1982). These effects are secondary consequences of the synaptic competition at the cortical level between geniculate fibers representing the deprived and the nondeprived eyes (Rauschecker, 1991). In pigeons and zebra finches, however, pre- or posthatch monocular deprivation affects somata in the optic tectum (Güntürkün, 1993; Manns & Güntürkün, 1999a), the n. rotundus (Herrmann & Bischof, 1986a; Manns & Güntürkün, 1999b), and the ectostriatum (Herrmann & Bischof, 1986b). While inputs of both eyes could compete at rotundal level, comparable competition is absent in the tectum and is unlikely in the ectostriatum. This suggests that visual deprivation effects in birds are mediated through activity-correlated effects within one hemisphere which possibly operate without direct synaptic competition between neurons representing deprived and nondeprived eyes.

A further difference of visual asymmetries in birds and mammals is the observation that in mammals only the unilateral absence of contoured visual patterns induces significant deprivation effects, while asymmetries of luminance alone do not lead to alterations (Movshon & Van Sluyters, 1981). This is generally taken as evidence that competitions between deprived and nondeprived sides are mediated by Hebbian mechanisms which require correlated activity of pre- and postsynaptic cells for stabilization or retraction of synapses (Cruikshank & Weinberger, 1996). In chicks and pigeons, the situation must be different since light has to shine through the eggshell and the closed lid of the embryo to induce asymmetries. Therefore, avian visual lateralization has to be induced by brightness and not by contoured visual pattern differences. Brightness differences are then probably coded by mere activity differences between the eyes and could induce asymmetries by the release of neurotrophins between the stimulated and the deprived hemisphere (Theiss & Güntürkün, 1998). Such activity-dependent trophic effects could generate the morphological left-right differences.

Morphological asymmetries are very likely powerful indicators for a lateralization of information processing. Thus, the functional dominance of one hemisphere seems to emerge from an asymmetrical embryonal position within the egg, which initiates a cascade of lateralized events which alter the morphology of the system and thereby induce a lateralization of visual processing.

VISUAL LATERALIZATION: STATIC OR DYNAMIC?

Thus far this article suggests that the emergence of visual lateralization in pigeons can be characterized as a short period in which tectofugal asymmetry develops in an activity-dependent manner. Alterations of the system would then only be possible during this transient period of plasticity, while asymmetry would be "static" and unmodifiable for the remaining lifetime. Several lines of evidence suggest this assumption of a static asymmetry to be

incomplete. If the tectal and the posterior commissures, which connect the tecta of both hemispheres, are transected, visual lateralization reverses to a left-eye dominance. This reversal of laterality is proportional to the number of transected fibers (Güntürkün & Böhringer, 1987). If a cerebral asymmetry is reversed by tectal commissurotomy, it is likely that this asymmetry was previously maintained at least in part by asymmetrical interactions between the tecta (but see Parsons & Rogers, 1993), which are known to primarily inhibit each other (Robert & Cuénod, 1969; Hardy et al., 1984). Keyserers et al. (1999) tested this hypothesis by recording field potentials from intratectal electrodes in response to a stroboscope flash to the contralateral eye and an electrical stimulation of the contralateral tectum. They found that the left tectum was able to modulate the flash-evoked potential of the right tectum to a larger extent than vice versa. This lateralized interhemispheric cross-talk could thus constitute an important "dynamic" component of asymmetric visual processing.

LATERALIZED HEMISPHERIC INTERACTIONS IN BIRDS

Experiments in chicks also suggest that interhemispheric interactions are asymmetric. If chicks are imprinted on an artificial object, the first critical neural processes to memorize this object's visual characteristics take place in the intermediate hyperstriatum ventrale (IMHV) (Horn, 1991). Lesion studies make it likely that within the first hours after imprinting the left IMHV projects multisynaptically onto the right IMHV to trigger the right IMHV's function of establishing storage of visual engrams of the imprinted object in further structures of the forebrain (McCabe et al., 1991). IMHV is also involved in one-trial passive-avoidance learning, with left IMHV having a dominant role in initial coding processes (Rose & Csillag, 1985). Lesion studies support a model in which the memory trace after training is not fixed to the left IMHV but "flows" within 1 h to right IMHV and from there subsequently to the limbic portion of the basal ganglia (Rose, 1991).

An asymmetric interhemispheric interaction was also found in food-storing marsh tits, which retrieve hoarded food many days after storing with astounding accuracy (Shettleworth, 1990). In these animals unilateral transfer to the left hemisphere occurs between 3 and 24 h, irrespective of which hemisphere had first access to this material (Sherry et al., 1981; Clayton, 1993).

It is not yet clear to what extent such differences are due to the species used, the stimulus material, or the way in which the stimulus material is processed. To further tackle this problem, which is crucial to an understanding of lateralized hemispheric interactions, we investigated the time course and lateralization of interhemispheric transfer in pigeons. Pigeons had been among the first animal species to be tested for interocular transfer, but a possible lateralization of this phenomenon was addressed only recently. The time course of interocular transfer in this species is largely unknown.

For several reasons, we tested for transfer of a simple color discrimination. First, numerous studies have employed color-discrimination tasks in testing for interhemispheric or interocular transfer. Thus, a sound database is available with which to compare the findings of the present study. Second, it is an easy task that is readily achieved within a single session so that predefined retention intervals could relatively strictly be adhered to. This is a very important point for transfer studies, since training over several sessions make it impossible to determine precisely at which point learning was achieved. Third, due to the relatively low cognitive demand of the task, lateralization of color-discrimination acquisition is virtually absent (Diekamp et al., 1999), making possible asymmetries of transfer easier to analyze.

MATERIALS AND METHODS

Animals

Thirty-six pigeons (*Columba livia*) from local domestic stock were used. They were maintained at 80% of their free feeding weights throughout the experiment and were experimentally naive for color/brightness-discrimination tasks. A ring of Velcro was fixed to the skin around their eyes with water-soluble nontoxic glue. Eyecaps made of cardboard were fitted and could easily be attached during monocular experimental sessions as needed.

Apparatus

The experimental chamber for pretraining and color-discrimination learning was a two-key operant chamber for pigeons (36 × 33 × 34 cm), illuminated by a house light. Response keys (diameter of 2 cm) were arranged vertically on the back panel with 4 cm between them and 16 and 24 cm distance to the floor. A feeder combined with a feeder light was located in the center of the back panel 5 cm above the floor. Pecking keys could be transilluminated by miniature lamps (24 V) with either white light for the training sessions or the different colors (green, blue, red, or yellow) used in the color discrimination. The colors were not matched for brightness. The experiment was controlled by a microcomputer equipped with a digital I/O board (CIO-PDISO8; Computer Boards, Inc.).

Training and Experimental Sessions

During training sessions one of the two operant keys was randomly illuminated with white light, while the other was dark. Animals were trained binocularly with white light as the correct stimulus until they reached a stable response rate of 90% correct responses in two consecutive sessions under a fixed ratio schedule (FR 2). Correct responses were reinforced with 3 s of access to grain, whereas incorrect choices resulted in a 5-s time-out with all lights turned off and no correction trial following. The intertrial interval (ITI) lasted 5 s. On the next day after successful completion of training sessions, experimental sessions began. In the *acquisition* phase pigeons learned a color discrimination under monocular conditions [either left-eye seeing (L) or right-eye seeing (R)]. In each trial the two pecking keys were both lit and the position of the two colors was randomized (Fellows, 1976). Correct and incorrect responses were reinforced as before. After reaching the criterion of 10 consecutive correct responses, a defined period (30, 60, 180, 480, or 1440 min) passed before the birds were tested on the same discrimination problem for *retention*. We adhered to these predefined intervals following some relevant studies in other avian species according to which memory formation begins

within minutes after training and is being transferred between the hemispheres between 3 and 24 h after the initial learning (Rose, 1991; Salinska et al., 1999; Clayton, 1993). The retention test phase was conducted with either the previously trained or the naive, previously untrained eye. Thus, according to the seeing condition during the acquisition and test phase, pigeons were divided into four groups. Pigeons in the "nontransfer" group were tested both times under the same monocular conditions either with the left eye or the right eye (L-L, R-R), whereas animals in the "transfer" group were tested under different monocular conditions in acquisition and retention (R-L, L-R).

A total of 96 experiments were run, which implies that some birds were tested up to three times. However, each bird was tested only once with a particular set of colors. A color learned as S+ in the first discrimination task could be S- in a further experiment, but only if combined with a new color. This procedure could be used, since all color combinations were balanced among eyecap groups and since the relevant variable was the efficiency of interocular transfer, which depended on transfer time and transfer direction.

Data Analysis

In order to determine T , which is the period of time between reaching criterion in the acquisition and regaining criterion in the test phase, two variables had to be considered. The first (T_{delay}) is the delay period between reaching criterion in the acquisition session and the start of the retention session (30, 60, 180, 480, or 1440 min), which is controlled by the experimenter. The second period (T_{animal}) is determined by the animals and varies considerably, depending on their pecking activity. For example, some animals did not respond for a long time at the beginning of a session, but then reached criterion within a few minutes. In this case, the predefined delay time would greatly underestimate the true retention and transfer time. Other animals are highly active at the beginning, then cease to respond for a lengthy time, and then start to be active again. Pecking activity was found to be highly variable in both transfer as well as nontransfer animals. To consider these differences in the activity distribution adequately, we added the time period T_{animal} to the a priori set delay time such that $T = T_{\text{animal}} + T_{\text{delay}}$; thus T_{animal} was defined as the point of time at which the medium peck of all pecks within a session occurred. The adjusted T values of all animals were used to define four different retention time intervals (30–50 min; 60–100 min; 180–250 min; 450–1470 min) based on a criterion of about an equal number of data points per time interval.

Although several individuals were tested with different eyecap conditions and/or different retention intervals, all data were treated as independent variables. This is justified because all animals were tested with one set of colors only once for acquisition. Performance in the retention phase was measured by the "number of trials needed to reach criterion" of 10 correct responses in series. As these behavioral measures were not normally distributed, separate Kruskal-Wallis ANOVAs were used for comparisons among the four experimental transfer groups and retention times followed by two-tailed Mann-Whitney U tests for between-groups analyses. Independent variables were the four transfer/nontransfer groups or the four retention intervals.

RESULTS

Acquisition

Pigeons acquired the given task easily within one training session, mastering the criterion within 93 ± 8.1 (mean \pm SEM) trials. There was no difference in the number of trials between the birds learning the task with their left or their right eye [$Z(R = 47, L = 49) = -.795; p = .426$; Mann-Whitney U test]. There was also no difference in the number of trials to reach criterion between animals performing the task for the first time and those that had previous

experience with other color combinations [$Z(1st = 35, Rep. = 61) = -.773$; $p = .439$]. Thus, although starting conditions differed among birds with respect to previous experience or color combination, there was no difference in acquisition performance related to left or right eye use.

Retention

As for the acquisition, there was no difference in the number of trials for birds performing the task for the first time or repeatedly [$Z(1st = 35, Rep. = 61) = -.825$; $p = .409$; Mann-Whitney U test]. In the retention test birds needed on average 34.4 ± 3.0 trials to criterion. Calculating the savings as percentages for each retention session of all birds [(trials in acquisition - trials in retention)/(trials in acquisition + trials in retention) $\times 100$], also called transfer index (Hamassaki & Britto, 1987; Watanabe, 1988), the average improvement of all birds accounts to an overall reduction in the number of trials to criterion by 38.9%. As compared to the nontransfer groups that showed on average 45.6% savings (R-R, 47.6%; L-L, 43.6%), both transfer groups reached similar saving measures with $31.5 \pm 6.6\%$ for the R-L group and $37.4 \pm 6.3\%$ for the L-R group.

Transfer conditions had a significant effect on performance as measured by the number of trials to criterion in the retention test (Fig. 2) [$H(3, N = 96) = 8.210$; $p = .042$; Kruskal-Wallis ANOVA], whereas the retention interval as such had no effect [$H(3, N = 96) = 4.920$; $p = .177$]. Comparisons between the four transfer groups yielded a difference in the number of trials to criterion for the L-R-shifted birds as compared to both nontransfer groups, i.e. a significant difference to the L-L [$Z(L-R = 30, L-L = 19) = -2.615$; $p = .009$; Mann-Whitney U test) and a marginally significant dif-

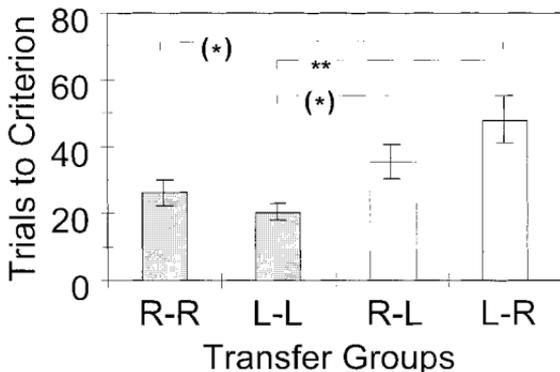


FIG. 2. Effects of transfer condition on the number of trials to criterion [$H(3, N = 96) = 8.210$; $p = .042$; Kruskal-Wallis ANOVA]. The mean number of cycles (\pm SEM) needed to criterion is shown for each of the four transfer groups (R-R, R-L, L-R, and L-L). L-R-shifted birds needed significantly more trials to criterion than each of the two nontransfer groups. Significance values represent the results of Mann-Whitney U tests [(*) $p < .100$; * $p < .050$; ** $p < .010$].

ference to the R-R group [$Z(\text{L-R} = 30, \text{R-R} = 19) = -1.801; p = .072$; Mann-Whitney U test].

Since the L-R-shifted group showed deficits in retraining criterion, we looked at this group more closely with respect to the retention interval. A Kruskal-Wallis ANOVA revealed significant effects of retention time on the number of trials to criterion [$H(3, \text{L-R} = 30) = 7.969; p < .047$] (Fig. 3). For this particular transfer group, performance was very low for retention times shorter than 50 min and improved with retention intervals between 3 and 4 h and longer. Differences in performance were significant between the 30- to 50-min retention interval and the long retention times of 180 - 250 min [$Z(\text{Ret 1} = 5, \text{Ret 3} = 5) = -2.619; p = .009$; Mann-Whitney U test] and the longest retention interval [$Z(\text{Ret 1} = 5, \text{Ret 4} = 9) = -2.069; p = .039$]. In addition, there was a clear trend toward improvement in performance between the 60- to 100-min interval and the 180- to 250-min interval [$Z(\text{Ret 2} = 11, \text{Ret 3} = 5) = -1.769; p = .077$]. A slight drop in performance occurred when comparing retention time of 3-4 h and an interval of 7.5 h and longer (Fig. 3).

Considering the low performance of the L-R group, in particular during short retention intervals, we compared their performance at the 30- to 50-min interval to that of the other transfer groups (Fig. 4). Overall effects of a Kruskal-Wallis ANOVA indicated significant differences between the four groups [$H(3, N = 26) = 8.281; p < .041$]. The L-R groups needed on average 70.2 ± 10.2 (mean \pm SEM) trials to criterion after the short retention period as compared to all other groups which mastered the task on average in less than 30 trials. Clearly, this difference in performance was significant between the L-R-shifted birds in comparison to all other groups (L-R vs R-R: $Z = -2.449, p = .0143$; L-R vs L-L: $Z = -2.679, p = .0073$; L-R vs R-L: $Z = -2.033, p = .042$; Mann-Whitney U tests).

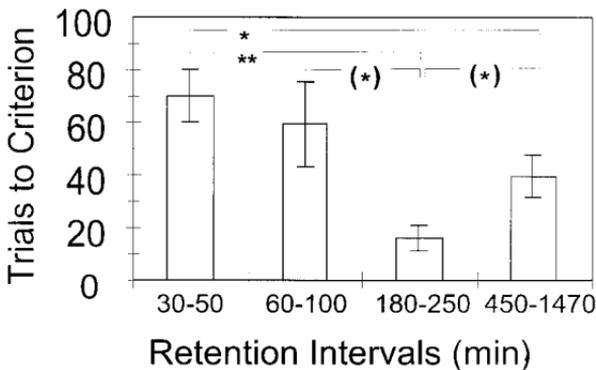


FIG. 3. Mean number of trials (\pm SEM) required by the L-R-shifted pigeons to reach criterion tested at four retention intervals. Effects of retention time were significant [$H(3, N = 30) = 7.969; p = .0467$; Kruskal-Wallis ANOVA] as more trials to criterion were needed after a short retention time than after retention periods of at least 3 h. Significance values represent the results of Mann-Whitney U tests [(*) $p < .100$; * $p < .050$; ** $p < .010$].

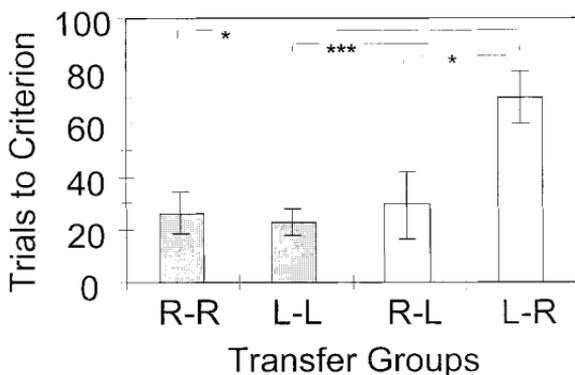


FIG. 4. Effects of transfer condition on retention performance 30–50 min after acquisition. The mean number of cycles (\pm SEM) needed to criterion is shown for each of the four transfer groups (R-R, R-L, L-R, and L-L). A Kruskal–Wallis ANOVA yielded significant group effects [$H(3, N = 26) = 8.281; p = .0406$]. L-R-shifted birds needed significantly more trials to criterion than all other groups. Significance values represent the results of Mann–Whitney U tests. [(*) $p < .100$; * $p < .050$; *** $p < .001$].

In order to evaluate the proficiency of transfer for the 30- to 50-min test interval, individual saving scores of the pigeons in transfer groups were divided by the mean savings of the nontransfer birds, which was 40.8% (Fig. 5). Using this measurement of the quality of interhemispheric transfer, a Kruskal–Wallis ANOVA indicated significant effects [$H(2, N = 26) = 9.938; p = .007$]. Compared to intrahemispheric consolidation of the non-

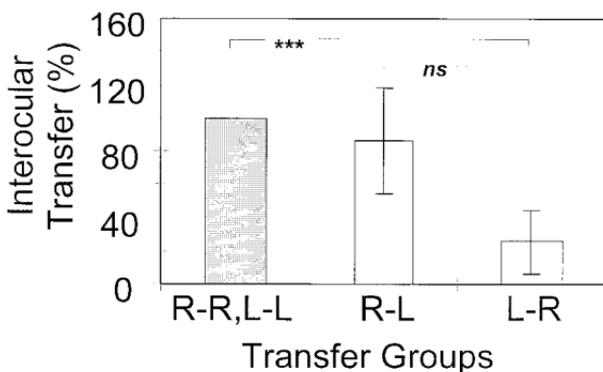


FIG. 5. Relative amount of interhemispheric savings (mean \pm SEM) as compared to the mean saving score of the nontransfer group (R-R and L-L) 30–50 min after acquisition. Savings [(acquisition trials – retention trials)/(acquisition trials – retention trials) \times 100] of the nontransfer groups are calculated in percentages relative to the mean savings of the nontransfer groups (100%). A Kruskal–Wallis ANOVA yielded significant group effects [$H(2, N = 26) = 9.938; p = .007$] with differences between the L-R-shifted birds and the nontransfer groups but not between the R-L and nontransfer birds. Significance values represent the results of Mann–Whitney U tests [*** $p < .001$; ns, nonsignificant].

transfer groups (defined as 100%) interocular transfer values of the L-R-shifted pigeons reached only $26.1 \pm 19.2\%$ [$Z(\text{No-Transfer} = 14, \text{L-R} = 5) = -4.180$; $p < .001$; Mann-Whitney U test], whereas R-L-shifted birds already had reached an interocular transfer rate of $86.6 \pm 31.3\%$ [$Z(\text{no-Transfer} = 14, \text{R-L} = 7) = -.622$; $p = .554$]. Although these differences in the transfer values between the L-R- and R-L-shifted birds failed to reach significance [$Z(\text{L-R} = 5, \text{R-L} = 7) = -1.542$; $p = .123$], the difference in the efficiency of interocular transfer between these two groups amounted to about 60%.

DISCUSSION

Our results provide evidence that interhemispheric transfer of color discrimination occurs in both directions but asymmetrically within the first hour after acquisition. For pigeons which learned the task monocularly, transfer was slower from the left to the right eye up to 50 min after acquisition than vice versa. For intervals longer than 3 h, no differences between right to left and left to right transfer and nontransfer groups were found. For the left- to right-eye-shifted animals measures within the 60- to 100-min interval varied greatly among individuals. Overall, these data show that each hemisphere shifts the stored information to the contralateral side, but the efficiency of this process is time and side dependent. At least within the time frame of 24 h tested, the stored memory trace did not disappear.

Findings of our present study are fairly consistent with results in chicks showing a more successful interocular transfer from the right eye system to the left than in the opposite direction. This has been shown for a one-trial passive-avoidance bead task (Sandi et al., 1993; Rose, 1991), an operant visual pattern-discrimination task (Gaston, 1984), as well as for imprinting studies (Horn, 1991). Thus, a similar kind of interocular transfer of a visual discrimination was found in avian species from two different orders. A deviating transfer pattern is found in food-storing marsh tits. Experiments in which these animals stored food using either the left or the right eye showed good performance after 24 h only when using the right eye/left hemisphere system. There was no transfer of information after a retention interval of 3 h (Sherry et al., 1981; Clayton, 1993). This means that a unilateral interhemispheric memory transfer occurred during the retention interval of 24 h from the right to the left hemisphere. Although phylogenetic factors cannot be ruled out as a possible explanation, it seems to be more likely that differences in interocular transfer patterns can be explained by the different types of cognitive processes required in these tasks. The food-storing tasks demand the animals to utilize spatial cues to find the correct site. Since studies in chicks could reveal a right-hemisphere dominance in spatial coding (Rashid & Andrew, 1989; Vallortigara et al., 1996), the brain mechanisms for

learning a color discrimination and those required for spatial learning are different (Vallortigara, 1988). The preferential transfer of storing information from the right to the left hemisphere in marsh tits therefore represent a shift of engrams from the (spatially) dominant to the subdominant half-brain. In principle this resembles the results of the present study in which the initial transfer occurs from the left hemisphere, which is dominant for visual object features, to the right. Since in pigeons, IOT of intensity and color information has been shown to occur (Francesconi et al., 1982; Watanabe et al., 1986) and since the left hemisphere is involved in color- as well as in brightness-discrimination tasks, we assume that the data would apply equally if the pigeons in this study would have used brightness instead of color of the stimuli. As findings from the present and other studies show, there appears to be a gradient in the occurrence of interhemispheric transfer from zero to almost perfect. As in this study, simultaneous color or pattern discriminations have produced successful interocular transfer in other experiments with pigeons (Watanabe, 1986; Diekamp et al., 1999), whereas in a spatial conditional discrimination task no successful transfer was observed (Green et al., 1978). Such discrepancies have brought about a vivid discussion about the essential prerequisites for the transmission of a learned visual information. Watanabe (1986) suggested the spatial separation of the discriminative stimulus and the pecking key to be decisive for IOT absence and suggested successful transfer to be inhibited if a visual signal has to be integrated with a motor response. Goodale and Graves (1981), on the other side, suggested that differences in retinal locus with which lateral versus binocular fixation is achieved is crucial for transmission. Analogous to IOT results in pigeons, there are dissenting findings in chicks caused by procedural variations within experimental designs. IOT was successful in a pattern-discrimination task when rewarded with food (Gaston, 1984), but not when reinforced with warm air (Gaston, 1979). This very short overview shows that cerebral asymmetries but also a multitude of further variables determine if interhemispheric transmission occurs. Against this background of data, we are inclined to believe that interhemispheric transfer is not by any means a passive conduction line but an active filter through which only selected processes may flow.

ASYMMETRIC SENSORY REPRESENTATIONS AND LATERALIZED TRANSFER

It is conceivable that the lateralized interhemispheric transfer after monocular acquisition of the color discrimination is related to the asymmetry of visual representation in the *n. rotundus*, which results from lateralized tectoro-tundal projections (Fig. 1). In the first phase of the IOT test, the acquisition, the *n. rotundus*, and further tectofugal structures contralateral to the used eye are predominantly involved with visual analysis and information storage.

In the second phase, the IOT test with the "naive" eye, three phenomena contribute to performance: new learning relayed by the "naive" rotundus not involved in acquisition, true interhemispheric transfer, and accessibility of information from the ipsilateral "experienced" rotundus. Due to the asymmetric tectal projections to the rotundus (Güntürkün et al., 1998; Fig. 1), more information from the acquisition phase should be available to a "naive" left eye than to a "naive" right eye after eyecap switch. Taken together, IOT from right eye to left eye should be facilitated due to a higher bilateral visual representation of the left-sided tectofugal system.

Possibly, asymmetrical representations and asymmetries of interhemispheric transfer are general properties of lateralizations in many species, including humans. Several studies have reported that visuospatial attentional tasks are associated with an activation of the dominant right superior parietal lobe after left- and right-sided attentional shifts, while the subdominant left hemisphere is, if at all, only active while attending to contralateral right stimuli (Corbetta et al., 1993; Vandenberghe et al., 1997). Consequently, some patients with right parietal lesions neglect target stimuli in both hemifields, while left-sided lesions only lead to mild contralateral impairments (Weintraub & Mesulam, 1988). A mirror-image pattern is observed for hand motor control. In right-handers, motor areas of the dominant left hemisphere are activated during left and right hand movements, while the subdominant right hemisphere is only involved in left hand motions (Durwen & Herzog, 1992, Herzog & Durwen, 1993, Kim et al., 1993). In left-handers, the dominant right premotor area is activated after finger movements on either side while the left premotor area is only involved in contralateral movements (Kawahima et al., 1997). Some right-handed patients with alien hand syndrome and hemispheric disconnection are unable to cross the body axis with the left hand, while being able to reach in whatever space position using the right (Nagumo et al., 1993). Again, these patterns might be related to a bilateral manual space representation in the dominant left motor cortex, while representation is only contralateral in the subdominant right motor cortex.

These asymmetries of representation could mediate some of the lateralizations of interhemispheric transfer which have been shown in humans. Marzi et al. (1991), performing a meta-analysis of different lateralized reaction-time tasks, concluded that visuomotor information transmission was faster from the right to the left hemisphere. This finding has recently been supported by Novicka et al. (1996), who showed that, for certain stimuli, interhemispheric transmission time was shorter for information transfer from the unspecialized hemisphere to the specialized one than transfer in the opposite direction. An especially elegant demonstration of this effect comes from Nalcaçi et al. (1999), who analyzed the frequency components of visual evoked potentials elicited by the reversal of checkerboard patterns presented in visual half-fields. Especially the activation of fibers contributing to the theta band were significantly faster from the right to the left hemisphere. Taken

together these results suggest that asymmetries of interhemispheric transfer may be a widespread phenomenon which could represent a key principle in the maintenance of lateralizations.

SUMMARY AND OUTLOOK

As argued at the beginning, one reason to work with animal models in asymmetry research is to solve the *fundamental* problems in lateralization research. One of these problems is the ontogeny of asymmetries. A further one is the neural mechanisms with which anatomical asymmetries are translated into lateralized functions. Studies on the visual system of chicks and pigeons are able to clarify some aspects of these questions.

In pigeons, visual feature detection is dominated by the tectofugal system of the left hemisphere. Ontogenetically, this lateralization starts with a genetic predisposition (embryonic asymmetrical position), which leads to an epigenetic effect (asymmetrical light stimulation). Brightness differences between the eyes result in activity differences between the ascending tectofugal pathways of the left and the right hemispheres, which are then transcribed during a critical time span into morphological asymmetries. After the end of this transient period, the established asymmetries determine the lateralized processes of the visual system for the entire life span of the individual.

As shown in the present study, these anatomical or "static" asymmetries produce or are at least accompanied by "dynamic" coding principles during visual learning processes. These principles enable a fast interocular and thus possibly interhemispheric transfer from the dominant right to the subdominant left eye. It will be exciting to analyze, in future studies, if a lateralized interhemispheric transfer, as shown in pigeons and various other species including humans, is indeed achieved by asymmetries of representation as suggested for the tectofugal system.

ACKNOWLEDGMENTS

This research was supported by the Deutsche Forschungsgemeinschaft through its Sonderforschungsbereich 509 NEUROVISION as well as by the prize of the Alfred Krupp Stiftung to O.G.

REFERENCES

- Alonso, Y. (1998). Lateralization of visual guided behaviour during feeding in zebra finches (*Taeniopygia guttata*). *Behavioural Processes*, **43**, 257–263.
- Broca, P. (1865). Sur le siège de la Faculté du langage articulé. *Bulletin de la Societe de Anthropologie* (Paris), **6**, 377–393.
- Chiarello, C., & Maxfield, L. (1996). Varieties of interhemispheric inhibition, or how to keep a good hemisphere down. *Brain and Cognition*, **30**, 81–108.
- Clayton, N. S. (1993). Lateralization and unilateral transfer of spatial memory in marsh tits. *Journal of Comparative Physiology A*, **171**, 799–806.

- Clayton, N. S., & Krebs, J. R. (1993). Lateralization in Paridae: Comparison of a storing and a non-storing species on a one-trial associative memory task. *Journal of Comparative Physiology A*, **171**, 807–815.
- Clayton, N. S., & Krebs, J. R. (1994). Memory for spatial and object-specific cues in food-storing and non-storing birds. *Journal of Comparative Physiology A*, **174**, 371–379.
- Corbetta, M., Miezin, F. M., Shulman, G. L., & Petersen, S. E. (1993). A PET study of visuo-spatial attention. *Journal of Neuroscience*, **13**, 1202–1226.
- Cruikshank, S. J., & Weinberger, N. M. (1996). Evidence for the Hebbian hypothesis in experience-dependent physiological plasticity of neocortex: A critical review. *Brain Research Reviews*, **22**, 191–228.
- Davidson, R. J., & Hugdahl, K. (Eds.) (1995). *Brain asymmetry*. Cambridge, MA: MIT Press.
- Diekamp, B., Prior, H., & Güntürkün, O. (1999). Lateralization of serial color reversal learning in pigeons (*Columba livia*). *Animal Cognition*, **2**, 187–196.
- Durwen, H. F., & Herzog, G. H. (1992). Electromyographic investigation of mirror movements in normal adult. *Developmental Brain Dysfunction*, **5**, 310–318.
- Engelage, J., & Bischof, H.-J. (1993). The organization of the tectofugal pathway in birds: A comparative review. In H. P. Zeigler & H.-J. Bischof (Eds.), *Vision, brain, and behavior in birds* (pp. 137–158). Cambridge, MA: MIT Press.
- Engelage, J., & Bischof, H.-J. (1988). Enucleation enhances ipsilateral flash evoked responses in the ectostriatum of the zebra finch (*Taeniopygia guttata castanotis* Gould). *Experimental Brain Research*, **70**, 79–89.
- Fellows, B. J. (1976). Chance stimulus sequences for discrimination tasks. *Psychological Bulletin*, **67**, 87–92.
- Francesconi, W., Fogassi, L., & Musumeci, D. (1982). Interocular transfer of visual discriminations in Wulst-ablated pigeons. *Behavioral Brain Research*, **5**, 399–406.
- Gaston, K. E. (1979). Lack of interocular transfer of pattern discrimination learning in chicks. *Brain Research*, **171**, 339–343.
- Gaston, K. E. (1984). Interocular transfer of pattern discrimination learning in chicks. *Brain Research*, **310**, 213–221.
- Goodale, M. A., & Graves, J. A. (1981). Interocular transfer in the pigeon: retinal locus as a factor. In D. J. Ingle, R. J. W. Mansfield, & M. A. Goodale (Eds.), *Analysis of visual behavior* (pp. 211–240). Cambridge, MA: MIT Press.
- Graves, J. A., & Goodale, M. A. (1977). Failure of interocular transfer in the pigeon (*Columba livia*). *Physiology and Behavior*, **19**, 425–428.
- Green, L., Brecha, N., & Gazzaniga, M. S. (1978). Interocular transfer of simultaneous but not successive discriminations in the pigeon. *Animal Learning and Behavior*, **6**, 261–264.
- Güntürkün, O. (1985). Lateralization of visually controlled behavior in pigeons. *Physiology and Behavior*, **34**, 575–577.
- Güntürkün, O. (1993). The ontogeny of visual lateralization in pigeons. *German Journal of Psychology*, **17**, 276–287.
- Güntürkün, O. (1997a). Avian visual lateralization—A review. *NeuroReport*, **6**, iii–xi.
- Güntürkün, O. (1997b). Visual lateralization in birds: From neurotrophins to cognition? *European Journal of Morphology*, **35**, 290–302.
- Güntürkün, O. (1997c). Morphological asymmetries of the tectum optimum in the pigeon. *Experimental Brain Research*, **116**, 561–566.
- Güntürkün, O., & Böhringer, P. G. (1987). Reversal of visual lateralization after midbrain commissurotomy in pigeons. *Brain Research*, **408**, 1–5.
- Güntürkün, O., & Hahmann, U. (1994). Visual acuity and hemispheric asymmetries in pigeons. *Behavioural Brain Research*, **60**, 171–175.

- Güntürkün, O., & Hahmann, U. (1999). Functional subdivisions of the ascending visual pathways in the pigeon. *Behavioural Brain Research*, **98**, 193–201.
- Güntürkün, O., Hellmann, B., Melsbach, G., & Prior, H. (1998). Asymmetries of representation in the visual system of pigeons. *NeuroReport*, **9**, 4127–4130.
- Güntürkün, O., & Hoferichter, H. H. (1985). Neglect after section of a left telencephalotectal tract in the pigeon. *Behavioural Brain Research*, **18**, 1–9.
- Güntürkün, O., & Kesch, S. (1987). Visual lateralization during feeding in pigeons. *Behavioral Neuroscience*, **101**, 433–435.
- Güntürkün, O., & Kischkel, K.-F. (1992). Is visual lateralization sex-dependent in pigeons? *Behavioural Brain Research*, **47**, 83–87.
- Hamassaki, D. E., & Britto, L. R. (1987). Interocular transfer of habituation in pigeons: Mediation by tectal and/or posterior commissures. *Behavioural Brain Research*, **23**, 175–179.
- Hardy, O., Leresche, N., & Jassik-Gerschenfeld, D. (1984). Postsynaptic potentials in neurons of the pigeon's optic tectum in response to afferent stimulation from the retina and other visual structures. *Brain Research*, **311**, 65–74.
- Hellige, J. B. (1993). *Hemispheric asymmetry: What's right and what's left*. Cambridge, MA: Harvard Univ. Press.
- Hellmann, B., & Güntürkün, O. (1999). Visual field specific heterogeneity within the tectofugal projection of the pigeon. *European Journal of Neuroscience*, **11**, 1–18.
- Herrmann, K., & Bischof, H. J. (1986a). Effects of monocular deprivation in the nucleus rotundus of zebra finches: A Nissl and deoxyglucose study. *Experimental Brain Research*, **64**, 119–126.
- Herrmann, K., & Bischof, H. J. (1986b). Monocular deprivation affects neuron size in the ectostriatum of the zebra finch brain. *Brain Research*, **379**, 143–146.
- Herzog, G. H., & Durwen, H. F. (1993). Electromyographic investigation of mirror movements in normal adults: Variation of frequency with stimulus modality. *Developmental Brain Dysfunction*, **6**, 329–336.
- Horn, G. (1991). Imprinting and recognition memory; a review of neural mechanisms. In R. J. Andrew (Ed.), *Neural and behavioral plasticity: The domestic chick as a model*, (pp. 219–261). Oxford, UK: Oxford Univ. Press.
- Kawashima, R., Inoue, K., Sato, K., & Fukuda, H. (1997). Functional asymmetry of cortical motor control in left-handed subjects. *NeuroReport*, **8**, 1729–1732.
- Keyser, C., Diekamp, B., & Güntürkün, O. (2000). Evidence for physiological asymmetries in the physiological intertectal connections of the pigeon (*Columba livia*) and their potential role in brain lateralisation. *Brain Research*, **852**, 406–413.
- Kim, S. G., Ashe, J., Hendrich, K., Ellermann, J. M., Merkle, H., Ugurbil, K., & Georgopoulos, A. P. (1993). Functional magnetic resonance imaging of motor cortex: Hemispheric asymmetry and handedness. *Science*, **261**, 615–617.
- Kuo, Z. Y. (1932). Ontogeny of embryonic behavior in Aves. III. The structural and environmental factors in embryonic behavior. *Journal Comparative Psychology*, **13**, 245–271.
- Manns, M. (1998). Die Ontogenese Visueller Lateralisation bei der Taube (*Columba livia*): Entwicklung und Plastizität des Systems. Ph.D. thesis, Fakultät für Psychologie, Ruhr-Universität Bochum.
- Manns, M., & Güntürkün, O. (1997). Development of the retinotectal system in the pigeon: A cholera toxin study. *Anatomy and Embryology*, **195**, 539–555.
- Manns, M., & Güntürkün, O. (1999). Monocular deprivation alters the direction of functional and morphological asymmetries in the pigeon's (*Columba livia*) visual system. *Behavioral Neuroscience*, **113**, 1257–1266.

- Manns, M., & Güntürkün, O. (1999b). 'Natural' and artificial monocular deprivation effects on thalamic soma sizes in pigeons. *NeuroReport*, **15**, 3223–3228.
- Martinoya, C., Le Houezec, J., & Bloch, S. (1988). Depth resolution in the pigeon. *Journal of Comparative Physiology*, **163**, 33–42.
- Marzi, C. A., Bisiacchi, P., & Nicoletti, R. (1991). Is interhemispheric transfer of visuomotor information asymmetric? Evidence from a meta-analysis. *Neuropsychologia*, **29**, 1163–1177.
- McCabe, B. J., & Horn, G. (1991). Synaptic transmission and recognition memory: Time course of changes in *N*-methyl-D-aspartate receptors after imprinting. *Behavioral Neuroscience*, **105**, 289–294.
- Mench, J. A., & Andrew, R. J. (1986). Lateralization of a food search task in the domestic chick. *Behavioral and Neural Biology*, **46**, 107–114.
- Moscovitch, M. (1983). Stages of processing and hemispheric differences in language in the normal subject. In M. Studdert-Kennedy (Ed.), *Psychobiology of language* (pp. 88–104). Cambridge, MA: MIT Press.
- Movshon, J. A., & Van Sluylers, R. C. (1981). Visual neural development. *Annual Review of Psychology*, **32**, 477–522.
- Nagumo, T., Yamadori, A., Soma, Y., Kayamori, R., & Ito, M. (1993). Crossed avoiding reaction: A disturbance of the manual spatial function. *Journal of Neurology, Neurosurgery, and Psychiatry*, **56**, 552–555.
- Nalcaci, E., Basar-Eroglu, C., & Stadler, M. (1999). Visual evoked potential interhemispheric transfer time in different frequency bands. *Clinical Neurophysiology*, **110**, 71–81.
- Nowicka, A., Grabowska, A., & Fersten, E. (1996). Interhemispheric transmission of information and functional asymmetry of the human brain. *Neuropsychologia*, **34**, 147–151.
- Parsons, C. H., & Rogers, L. J. (1993). Role of the tectal and posterior commissures in lateralization of the avian brain. *Behavioral Brain Research*, **54**, 153–164.
- Rashid, N., & Andrew, R. J. (1989). Right hemisphere advantage for topographic orientation in the domestic chick. *Neuropsychologia*, **27**, 937–948.
- Rauschecker, J. P. (1991). Mechanisms of visual plasticity: Hebb synapses, NMDA receptors, and beyond. *Physiological Reviews*, **71**, 587–615.
- Regard, M., Cook, N. D., Wieser, H. G., & Landis, T. (1994). The dynamics of cerebral dominance during unilateral limbic seizures. *Brain*, **117**, 91–104.
- Regard, M., Landis, T., Wieser, H. G., & Hailer, M. (1985). Functional inhibition and release: Unilateral tachistoscopic performance and stereoelectro-encephalographic activity in a case with left limbic status epilepticus. *Neuropsychologia*, **23**, 431–435.
- Remy, M., & Emmerton, J. (1991). Directional dependence of intraocular transfer of stimulus detection in pigeons (*Columba livia*). *Behavioral Neuroscience*, **105**, 647–652.
- Remy, M., & Güntürkün, O. (1991). Retinal afferents of the tectum opticum and the nucleus opticus principalis thalami in the pigeon. *Journal of Comparative Neurology*, **305**, 57–70.
- Ringo, J. L. (1990). Interhemispheric transfer of visual discriminations in split-chiasm monkeys (*Macaca nemestrina*) and its measurement. *Behavioral Neuroscience*, **104**, 900–905.
- Robert, F., & Cuénod, M. (1969). Electrophysiology of the intertectal commissures in the pigeon. II. Inhibitory interaction. *Experimental Brain Research*, **9**, 123–136.
- Rogers, L. J. (1982). Light experience and asymmetry of brain function in chicken. *Nature*, **297**, 223–225.
- Rogers, L. J. (1990). Light input and the reversal of functional lateralization in the chicken brain. *Behavioural Brain Research*, **38**, 211–221.

- Rogers, L. (1996). Behavioral, structural and neurochemical asymmetries in the avian brain: A model system for studying visual development and processing. *Neuroscience and Biobehavioral Reviews*, **20**, 487–503.
- Rose, S. P. R., & Csillag, A. (1985). Passive avoidance training results in lasting changes in deoxyglucose metabolism in left hemisphere regions of chick brain. *Behavioral and Neural Biology*, **44**, 315–324.
- Rose, S. P. R., (1991). How chicks make memories: The cellular cascade from c-fos to dendritic remodelling. *Trends in Neurosciences*, **14**, 390–397.
- Salinska, E. J., Chaudhury, D., Bourne, R. C., & Rose, S. P. (1999). Passive avoidance training results in increased responsiveness of voltage- and ligand-gated calcium channels in chick brain synaptoneuroosomes. *Neuroscience*, **93**, 1507–1514.
- Sandi, C., Patterson, T. A., & Rose, S. P. (1993). Visual input and lateralization of brain function in learning in the chick. *Neuroscience*, **52**, 393–401.
- Sherman, S. M., & Spear, P. D. (1982). Organization of visual pathways in normal and visually deprived cats. *Physiological Reviews*, **62**, 738–855.
- Sherry, D. F., Krebs, J. R., & Cowie, R. J. (1981). Memory for the location of stored food in marsh tits. *Animal Behaviour*, **29**, 1260–1266.
- Shettleworth, S. J. (1990). Spatial memory in food-storing birds. *Philosophical Transactions of the Royal Society of London B*, **329**, 143–151.
- Shimizu, T., & Karten, H. J. (1993). The avian visual system and the evolution of the neocortex. In H. P. Zeigler & H.-J. Bischof (Eds.), *Vision, brain and behavior in birds* (pp. 103–114). Cambridge, MA: MIT Press.
- Theiss, C., & Güntürkün, O. (1998). NT-3 and trk C expression in the developing retinotectal system in pigeons. In N. Elsner & R. Wehner (Eds.), *Göttingen Neurobiology Report*, p. 489. Stuttgart: Thieme.
- Ulrich, C., Prior, H., Duka, T., Leshchins'ka, I. Valenti, P., Güntürkün, O., & Lipp, H.-P. (1999). Left-hemispheric superiority for visuospatial orientation in homing pigeons. *Behavioural Brain Research*, **104**, 169–178.
- Vallortigara, G. (1988). Behavioral asymmetries in visual learning of young chickens. *Physiology and Behavior*, **45**, 797–800.
- Vallortigara, G., Regolin, L., Bortolomioli, G., & Tommasi, L. (1996). Lateral asymmetries due to preferences in eye use during visual discrimination learning in chicks. *Behavioral Brain Research*, **74**, 135–143.
- Vandenbergh, R., Duncan, J., Dupont, P., Ward, R., Poline, J.-B., Bormans, G., Michiels, J., Mortelmans, L., & Orban, G. A. (1997). Attention to one or two features in left or right visual field: A PET study. *Journal of Neuroscience*, **17**, 3739–3750.
- Von Fersen, L., & Güntürkün, O. (1990). Visual memory lateralization in pigeons. *Neuropsychologia*, **28**, 1–7.
- Watanabe, S. (1986). Interocular transfer of learning in the pigeon: Visuo-motor integration and separation of discriminanda and manipulanda. *Behavioural Brain Research*, **19**, 227–232.
- Watanabe, S. (1988). Effects of unilateral thalamic lesion upon interocular transfer of visual discrimination in pigeons. I. Lesion in the trained hemisphere (memory access deficits). *Behavioural Brain Research*, **29**, 259–265.
- Weidner, C., Reperant, J., Miceli, D., Haby, M., & Rio J. P. (1985). An anatomical study of ipsilateral retinal projections in the quail using radioautographic, horseradish peroxidase, fluorescence and degeneration techniques. *Brain Research*, **340**, 99–108.
- Weintraub, S., & Mesulam, M. M. (1988). Visual hemispatial inattention: stimulus parameters and exploratory strategies. *Journal of Neurology, Neurosurgery, and Psychiatry*, **51**, 1481–1488.