

ORIGINAL ARTICLE

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Functional lateralization, interhemispheric transfer and position bias in serial reversal learning in pigeons (*Columba livia*)

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Abstract In the present study we investigated lateralization of color reversal learning in pigeons. After monocular acquisition of a simple color discrimination with either the left or right eye, birds were tested in a serial reversal procedure. While there was only a slight and non-significant difference in choice accuracy during original color discrimination, a stable superiority of birds using the right eye emerged in serial reversals. Both groups showed a characteristic ‘learning-to-learn’ effect, but right-eyed subjects improved faster and reached a lower asymptotic error rate. Subsequent testing for interocular transfer demonstrated a difference between pre- and post-shift choice accuracy in pigeons switching from right to left eye but not vice versa. This can be accounted for by differences in maximum performance using either the left or right eye along with an equally efficient but incomplete interocular transfer in both directions. Detailed analysis of the birds’ response patterns during serial reversals revealed a preference for the right of two response keys in both groups. This bias was most pronounced at the beginning of a session. It decreased within sessions, but became more pronounced in late reversals, thus indicating a successful strategy for mastering the serial reversal task. Interocular transfer of response patterns revealed an unexpected asymmetry. Birds switching from right to left eye continued to prefer the right side, whereas pigeons shifting from left to right eye were now biased towards the left side. The results suggest that lateralized performance during reversal learning in pigeons rests on a complex interplay of learning about individual stimuli, stimulus dimensions, and lateralized response strategies.

Key words Birds · Hemispheric asymmetries · Interocular transfer · Discrimination learning

Introduction

Functional and anatomical asymmetries are not only an attribute of human brains but likewise are found in many different non-primate species. The avian visual system, in particular, has emerged as an excellent model for the study of hemispheric specialization (Andrew 1983; Mench and Andrew 1986; Vallortigara and Andrew 1994; Rogers 1995; Vallortigara et al. 1996; Güntürkün 1997a). Because of the almost complete decussation of the optic nerves in birds, each hemisphere receives input predominantly from the contralateral eye (Weidner et al. 1985), although a small amount of fibers recross in the supraoptic, posterior and tectal commissures (Güntürkün et al. 1993; Bischof and Watanabe 1997). Functional aspects of each hemisphere and significant asymmetries can be revealed by covering one eye with an eyecap and thus directing the flow of information primarily to one half of the bird’s brain. Consequently, any differences in performance under right eye or left eye seeing conditions are most likely due to differences in the manner in which each hemisphere processes various tasks. Lateralization is based on central, neural mechanisms, since differences in performance under monocular left or right eye conditions are not caused by peripheral factors such as differences in visual acuity, wavelength discrimination or depth resolution (Martinoya et al. 1988; Remy and Emmerton 1991; Güntürkün and Hahmann 1994). In addition, unilateral lesions or injections of glutamate into visual structures of the visual tectofugal or thalamofugal pathway have lateralized effects on different types of visually guided behavior and discrimination performance (Deng and Rogers 1997; Güntürkün and Hahmann 1999).

A considerable body of data has accumulated showing a robust advantage of the right eye (right eye/left hemisphere system according to Andrew [1991]) in visual dis-

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crimination tasks. Pigeons, young chicks and zebra finches achieve higher performance with their right eye when tested in an ecologically relevant discrimination task, the grain-grit or pebble-floor task, respectively (Hambley and Rogers 1979; Rogers and Anson 1979; Mench and Andrew 1986; Güntürkün and Kesch 1987; Alonso 1998). This right eye advantage also exists for the discrimination of abstract stimuli and for the retention of a large number of different patterns (Gaston and Gaston 1984; Güntürkün 1985; von Fersen and Güntürkün 1990). Moreover, the right eye system is bluffed more easily than the left eye by the herringbone illusion (Güntürkün 1997b). Whereas performance differences were relatively small in some of these discriminations, particularly marked interhemispheric differences emerged in studies requiring large memory capacity (von Fersen and Güntürkün 1990) or additional and higher order processing capacity as in spatial conditional pattern discrimination and perception of the herringbone illusion (Güntürkün 1997b). This suggests that cerebral asymmetries reflect the unilateral existence of neural modules which either have surplus processing capacity, such that specific information is analyzed faster, or which provide task-specific algorithms so that the solution of a problem becomes the domain of one hemisphere.

To further investigate this hypothesis, we tested pigeons for lateralization of serial color reversal learning, a task that necessitates different and more complex cognitive mechanisms than a simple color discrimination. In serial color reversal learning, subjects first learn a simple discrimination. After fulfilling the criterion, they are required to repress responses to the rewarded stimulus and to respond to the previously unrewarded one. Upon fulfilling the criterion again, contingencies are reversed once more, and so on. Pigeons, like many other vertebrate species, manage to learn this task and improve with successive reversals (Gossette et al. 1966; Benowitz and Lee Teng 1973; Mackintosh et al. 1985; Chaves et al. 1993). After several successive reversals birds and mammals may develop a 'learning-to-learn' effect and very quickly change to the previously unrewarded color within the first trials of a new reversal session, whereas the goldfish, for example, is known to learn a reversal task without being able to achieve a learning set (Mackintosh et al. 1985; Davey 1989). We therefore assumed this cognitive component to be particularly demanding.

Aside from the fact that very few studies have so far investigated lateralization of color discrimination (Vallortigara 1989) but have not tested for lateralization of reversal learning in birds, we were interested in this paradigm, since it experimentally separates two fundamental components of discrimination learning, the learning about the relevant stimulus dimension and the learning about individual stimuli and their reward properties. During serial reversal learning, subjects have to attend to the same stimulus dimension (e.g. color or brightness) as during acquisition. By contrast, reward properties of individual stimuli (e.g. red, green or light, dark) have to be updated with each reversal. This means that a simple discrimination can be solved by means of a simple reference memory strat-

egy, whereas improvement during serial reversals additionally requires working memory-like processes that tell the subject which of two response options that share a similar overall history of positive and negative outcomes is valid at a certain time. That additional processing requirements can indeed reveal lateralized neural systems is indicated by a study on human 'split brains' in tactile serial reversal learning (Teng 1998). While there was no interhemispheric difference in the acquisition of a discrimination task, a profound superiority of the left hemisphere emerged during serial reversal learning.

In addition to performance during serial reversals, we intended to analyze possible asymmetries in the interocular (i.e. interhemispheric) transfer of information. Various studies have shown that interocular transfer does occur in birds in color or pattern discriminations (Catania 1965; Mello 1968; Green et al. 1978; Remy and Watanabe 1993), while other experiments reported a lack of transfer in paradigms which were sometimes only slightly altered (Green et al. 1978; Watanabe and Weiss 1984). At least part of these contradictions might arise due to asymmetries of transfer between the two hemispheres. Transfer asymmetries have been reported for spatial information in food-storing birds (Clayton 1993; Clayton and Krebs 1994), as well as for filial imprinting (Horn et al. 1982) and one-trial passive avoidance learning in young chicks (Rose 1991). Given the conflicting results of interocular transfer in different experimental designs and accounts of unequal hemispheric transfer based on the type of information, it remains to be clarified whether interocular transfer of learned behavioral strategies used in reversal learning occurs and whether this ability is transferred in both directions between the hemispheres.

The experimental paradigm in the present study involved repetitive serial color reversal training under the same monocular conditions, either right eye or left eye open, to study functional asymmetries of each hemisphere. After completion of 30 successful reversals the same task was performed with the previously occluded eye to investigate possible asymmetries in the direction of information transfer between the hemispheres.

Methods

Subjects

Subjects were 16 pigeons (*Columba livia*) aged 1–3 years obtained from local breeders. They were kept in individual cages in a temperature- and humidity-controlled room on a 12-h light/dark schedule. Throughout the experiment all subjects were food deprived to 80–85% of their free-feeding weights. Water was available ad libitum. All pigeons were naive subjects.

Apparatus

For pretraining and reversal learning two identically equipped two-key operant chambers ($34 \times 33 \times 36$ cm) were used which were controlled by a microcomputer with a digital I/O board (CIO-PDISO8; Computer Boards, Inc.). The operant keys were located on the back panel 24 cm above the floor, spaced 24 cm apart and 5 cm from the left or right corner. Each key was transilluminated either with white light for the pretraining sessions or red or green light during the experimental sessions. The colors were not matched for brightness. For simplicity we will refer to the task as a color and not a color/brightness discrimination task, although brightness instead of color might have been used as relevant cue. A feeder combined with a feeder light was located in the center of the back panel 5 cm above the floor.

Procedure

Pretraining

All pigeons were first trained under binocular conditions to peck reliably on one of two keys, whichever was illuminated with white light. The position of the illuminated key was randomized according to Fellows (1967). Following a correct response, the stimulus light extinguished and the pigeon was reinforced with 3-s access to food. A single peck on the incorrect key always resulted in a 5-s time-out period during which all chamber lights were turned off, including the lights of the operant keys. Training sessions consisted of 48 trials. Each trial was separated by a 5-s interval. The number of pecks required to trigger reinforcement was increased successively from one to three [fixed ratio (FR) 1–3]. The criterion for advancing from a pretraining schedule with a FR 1, then to a FR 2 and finally to a FR 3 was 80% correct responses in two subsequent sessions. Binocular pretraining continued until the animals fulfilled the criterion with a FR 3. Thereafter, they underwent surgery.

Animals were anesthetized with ketamine/xylazine (40 mg/kg; 8 mg/kg) and a small metal block with a tapped hole was fixed to the skull with dental acrylic. Following surgery and 2 days of recovery, pretraining resumed under monocular conditions. During the sessions, sight was restricted to either the right or left eye by means of an eyecap screwed to the metal block. Immediately after finishing each session, the eyecap was removed and birds were returned to their homecage. Pretraining under the FR 3 schedule proceeded under the right-eye seeing condition for half of the subjects and under the left-eye seeing condition for the other half until criterion was fulfilled again.

Color discrimination and reversal learning

Simultaneous color discrimination and reversal learning began under the same monocular condition as in pretrain-

ing. Each session consisted of 60 trials in which either the red or the green light was reinforced. The two operant keys were illuminated simultaneously, with the position of the colors changing randomly (Fellows 1967). Assignment to the right and left monocular group and initial color discrimination to a positive red or green stimulus was balanced amongst animals. For half of the subjects the red key was the positive stimulus in the first session; for the other half, it was the green key. As during pretraining, pigeons were reinforced with 3-s access to food according to a FR 3 schedule and punished with a 5-s time-out after one peck on the incorrect key. All animals were given one session per day. Learning criterion was 80% correct responses in one session. Upon fulfilling this criterion, the values of the two colors were reversed on the following day. All pigeons completed at least 30 reversal blocks under one monocular condition. Subsequently 12 subjects were tested under monocular conditions with the opposite eye for ten reversal blocks.

Results

Initial discrimination learning

The number of sessions and number of errors to fulfill the criterion on the initial color discrimination varied greatly among individuals. They needed between one and six sessions (on average 1.9 ± 0.4 (SE)) and the mean number of errors accumulated within these sessions was 0–55.1% (on average 15.7 ± 3.4). Animals seeing with their right eye learned the discrimination slightly faster, within 1.6 sessions, and accumulated on average $13.1 \pm 3.4\%$ errors whereas those seeing with their left eye needed 2.3 sessions and made on average $18.3 \pm 5.9\%$ errors. This minor right eye advantage for the acquisition of the color discrimination task, however, was not significant (*t*-test for independent samples, $t_{14} = 0.758$; $P = 0.461$).

Reversal learning

Two pigeons had great difficulties in learning the reversal task. Although they had learned the initial color discrimination within one and two sessions, respectively, they needed more than 20 sessions to reach criterion in the first reversal block. Starting with the third reversal they responded exclusively to the incorrect color in over ten sessions or stopped responding at all. Thus, data from these two animals, one right-eye-seeing and one left-eye-seeing bird, were excluded from the analysis.

Figure 1 shows the learning curve for several blocks of successive color reversals of one individual. For the first five reversal blocks this pigeon needed 15 sessions, 3 sessions each time, whereas for the subsequent reversals it only needed 1–2 sessions (with the exception of the ninth reversal). The error rate of the first session of each reversal block was very high for reversals 1–5 but dropped to

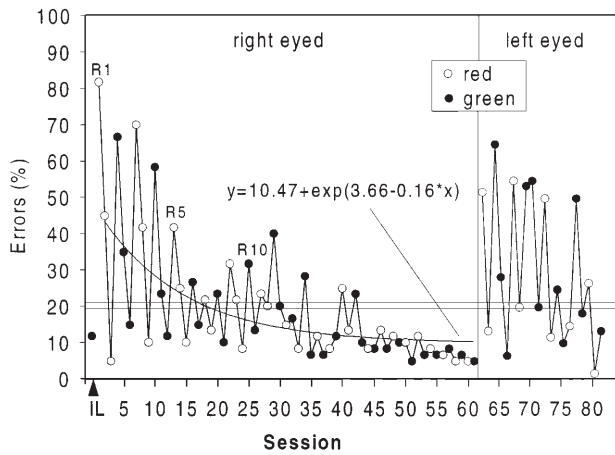


Fig. 1 Percent errors during successive sessions (60 trials) of an individual pigeon for initial learning (IL) of color discrimination, for 40 successive reversals of the task under monocular, right eye conditions and, subsequently, for 10 reversals under monocular left eye conditions. Each reversal block is marked with *black or white points* indicating two colors that were defined as positive stimulus during those sessions. The beginning of the first, fifth and tenth reversal block is indexed (R1, R5, R10). A new reversal started as soon as the criterion of less than 20% errors (*double line*) was reached within one session. The curve represented by a *thin line* is the best exponential fit to the data

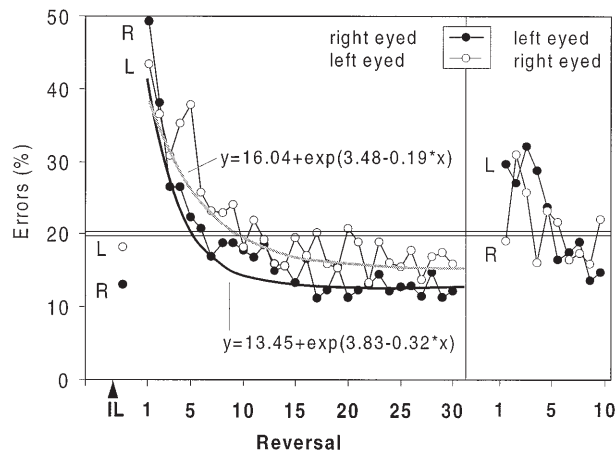


Fig. 2 Performance of the group of pigeons which was tested in a serial color reversal task for 30 reversals under monocular right eye conditions and afterwards in 10 reversals under left eye conditions (●) and of those pigeons that were first tested under left and then under right eye conditions (○). Mean number of errors (percent) was calculated based on the error rate accumulated for all sessions belonging to the same reversal block. The exponential functions that best fit the data are represented by *thin lines* (gray: left eye group; black: right eye group)

much lower levels over subsequent reversals. Although the number of sessions to complete 30 reversal blocks varied greatly between birds and reflected individual learning abilities, the shape of the learning curve for successive reversals was similar for all subjects.

At the first reversal all birds started out at about chance level with the right-eye-seeing group starting at an even higher error level ($49.3\% \pm 5.3$) than the left-eye-seeing

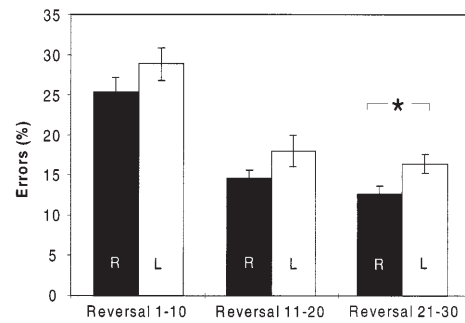


Fig. 3 Mean percent errors in blocks of 10 reversals of pigeons performing under right eye ($n = 7$) or left eye viewing conditions ($n = 7$). A 2×3 ANOVA of repeated measures indicated a significant right-eye versus left-eye group effect and a significant main effect of reversal number. In the third set the right eye group (R) achieved better scores than the left eye group (L) ($F_{1,12} = 5.98$; $P = 0.031$, one-tailed planned comparison). Error bars indicate standard errors

group ($45.5\% \pm 3.4$) (Figs. 1, 2). As for acquisition during the color discrimination task there was no significant difference in the performance of the two groups during this first reversal (t -test for independent samples, $t_{14} = 0.596$; $P = 0.562$). Within ten reversals error rates of both groups had dropped substantially to less than 20% and after repeated reversals had reached relatively stable values that fluctuated around 15%. The performance of reversal learning was summarized by calculating the average error rate over ten reversal blocks at a time (Fig. 3). A 2 (eye) \times 3 (reversals 1–10, 11–20 and 21–30) repeated measures analysis of variance indicated a significant main effect of the right versus left eye condition on overall performance ($F_{1,12} = 3.38$, $P < 0.046$, one-tailed according to our directional hypothesis). In addition, the results showed a significant main effect of the reversal session on performance ($F_{2,24} = 113.38$, $P < 0.001$, one-tailed), i.e. a learning-to-learn effect. The interaction was not significant. Since we were interested in differences in the performance between the two groups with an a priori expectation of a right eye advantage for this task we used planned comparisons to test this hypothesis. Although there were no significant performance differences between the two groups for reversal block 1–10 ($F_{1,12} = 1.67$, $P = 0.110$; one-tailed) and block 11–20 ($F_{1,12} = 2.45$, $P = 0.071$; one-tailed) the final performance in reversal 21–30 was significantly better for the right eye group ($F_{1,12} = 5.97$; $P = 0.016$; one-tailed). Error rates of the right eye group oscillated at around 12.7% compared to those of the left eye group, which were around 16.4%. Thus, although performance levels of the first reversal session and of the reversals at the beginning of the serial reversal training did not differ, birds performing the reversal task with the right eye finally outperformed the group seeing with their left eye (Figs. 2, 3).

As the learning process of each group is not comprehensively delineated by the improvement in performance over the three 10-reversal blocks we used a function of best fit for further analysis. Reversal learning can be de-

scribed best on a mathematical basis by an exponential function of the type $y = a + e^{(b-cx)}$ with a representing the asymptote, i.e. the error rate around which the performance oscillated after several reversals, b determining the starting value of the function for the first reversal and c representing the steepness of the curve, i.e. the rate of error reduction. Additional statistical analysis were thus performed on two of these variables that describe the effect and process of serial reversal learning. The constant value a is very similar to the mean performance during the last ten reversals and, accordingly, becomes significant (t -test for independent samples, $t_{12} = 2.62$, $P = 0.012$; one-tailed). It shows that the two groups differed in their best performance after repeated reversals. The other value c , which approximately matches the process or the rate of improvement during reversal learning, also indicated a right eye advantage for the learning-to-learn effect in reversal learning ($t_{12} = 2.21$, $P = 0.024$; one-tailed). The variable a , the starting point of the function during the first reversal, was not analyzed as it depends on the asymptotic value b . Based on these learning functions, we calculated the number of reversals each bird needed to reach at the 20% error level. Again, there was a significant difference in the number of reversal blocks to reach that level in favor of the right eye group ($t_{12} = 1.93$, $P = 0.039$, one-tailed).

Interhemispheric transfer of the reversal task

After completion of several color reversals, the eyecap was switched to cover the eye on the opposite side. Four of the animals that had finished the serial reversal task were not available for this second part of the study. Of the remaining animals data from two subjects were disregarded since they never fulfilled the criterion. One of these animals that had initially learned the reversal under right-eye-seeing conditions stopped responding at all in over 20 sessions after the eyecap had been switched from the left to the right eye. The other animal that first started out under left eye seeing conditions continued to respond to the discrimination task. However, this animal did not manage to fulfill the criterion with the right eye in 25 sessions but rather stayed at chance level with a maximum performance of only 58% correct responses.

All other animals accomplished the task under the opposite eye condition, but started at a higher error level or showed inconsistent behavior as compared to the steady and high level of performance they had previously reached with the other eye after 30 reversals (Figs. 1, 2). The mean error rate (\pm SE) for the last 10 reversal blocks before interocular transfer was $11.8\% \pm 1.2$ for animals tested monocularly right and $15.0\% \pm 1.3$ for those tested monocularly left. Birds initially seeing with their right eye that now switched to perform the reversal task with their left eye scored worse than before (Fig. 4). They made significantly more errors (on average $28.8\% \pm 4.3$) in the first reversal after interocular transfer as compared to the ten pre-transfer sessions (t -test for dependent samples,

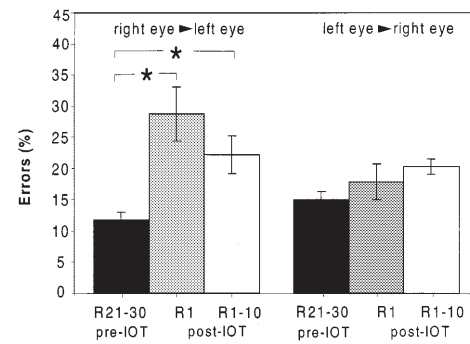


Fig. 4 Mean percent errors of pre- and post-interocular transfer reversal blocks. Pre-interocular transfer sessions contain reversal blocks 21–30, post-interocular transfer sessions cover the first reversal (R1) or reversal blocks 1–10, respectively, under the opposite seeing condition. One group of pigeons was switched from monocular right to left-eye-seeing condition, the other group from monocular left to right-eye seeing. Error bars indicate standard errors. Pigeons performing the reversal task initially with their right eye showed significant deficits after interocular transfer when using their left eye (t -test for dependent samples, $t_3 = 3.92$, $P < 0.029$; $t_3 = 3.72$, $P < 0.034$ for the first reversal or reversal blocks 1–10, respectively)

$t_3 = 3.92$, $P = 0.029$). Even over the course of ten post-transfer reversals the error rate was still $22.3\% \pm 3.0$ and double the error rate compared to the ten pre-transfer sessions ($t_3 = 3.72$, $P = 0.034$). Animals initially performing the task with their left eye and then with their right eye also made more errors after the transfer. But their post-transfer performance, with $17.9\% \pm 2.9$ errors in the first post-transfer reversal and $20.3\% \pm 1.2$ errors during ten post-transfer reversals, was not significantly different from their pre-transfer performance ($t_3 = 0.61$, $P = 0.582$; $t_3 = 2.58$, $P = 0.082$; respectively). Asymmetries in the reversal task between the right and left eye group observed before interocular transfer remained at about the same level. Based on the number of errors during ten reversal blocks before and after interocular transfer the difference in performance was about 3% and 2%, respectively, but always in favor of those birds performing the task with their right eye.

Side preferences

It became evident from observations during successive reversals that pigeons chose to peck preferentially at one response key, although the color defined as the correct stimulus was evenly and randomly distributed on left and right operant keys (Fig. 5). This response bias was analyzed by calculating the relative number of choices to the right and left response key over all trials [(responses to the right key – responses to the left key)/all responses]. Positive numbers indicate a preference for pecking activity to the right side, negative numbers a preference for the left side. Pigeons in both groups showed a preference for one side ($t_{29} = 6.60$, $P < 0.001$; $t_{29} = 13.01$, $P < 0.001$; for the right-eye and left-eye groups, respectively; one-sample t -test

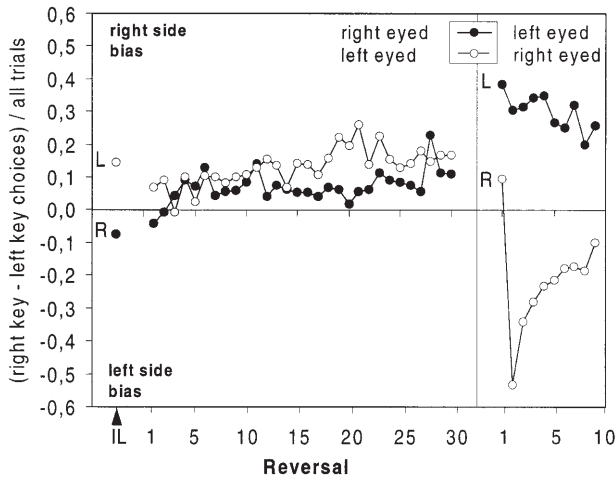


Fig. 5 Preference for a response key during serial reversals in pigeons trained monocularly right and left before and after switching eyecaps. Preferences were calculated as the number of choices made for the right response key minus those made for the left response key to all choices. Positive numbers indicate a preference for pecking activity to the right side and negative numbers indicate left side preferences

against zero), in particular for the right response key. This behavior was more distinct in pigeons seeing with their left eye than with their right eye. As this behavior might be affected by the side on which pigeons were able to view the stimulus, a statistical analysis was performed on the data with regard to the monocular viewing condition and the response key that was located on the side ipsilateral or contralateral to the open eye. A two-factor repeated measures analysis of variance over the initial 30 reversals indicated a significant effect of the left versus right eye condition on the preferred operant key. Right-eye-seeing pigeons preferentially chose the ipsilateral (right) response key whereas left-eye-seeing pigeons more often chose the contralateral (also right) response key ($F_{1,12} = 8.65, P < 0.013$). Thus, pigeons seeing with their right eye turned to the side of the uncovered eye, while animals seeing with their left eye preferentially chose the key on their “blind” side. This pattern changed after switching the eyecaps. Birds seeing with their left eye now preferred the right response key whereas birds using their right eye chose primarily the left response key. This bias initially was very pronounced after interocular transfer but gradually disappeared with successive reversals as pigeons improved in their overall performance.

Analysis of performance within sessions showed that side preferences were especially pronounced at the beginning of each session (Figs. 6, 7). Similar to the response bias over all trials a side preference was calculated for the initial 12 trials of each session [(responses to the right key – responses to the left key)/12]. The sequence of positions according to Fellows (1967) is a multiple of a 12-item sequence with an equal occurrence of correct right and left side stimuli during 12 trials. The mean response bias over all trials for the right-eye-seeing birds was 0.07 ± 0.02 (SE) but it was much stronger with a value of 0.18 ± 0.06

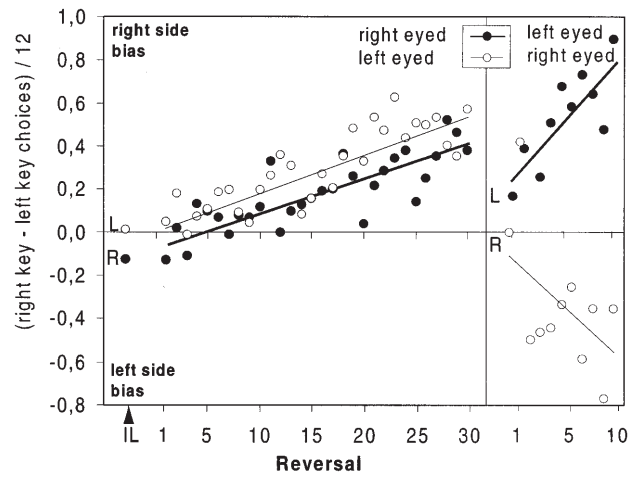


Fig. 6 Response key preference during the first 12 trials of each session. Preferences were calculated as the number of right key minus left key choices during the first 12 trials. Positive numbers indicate a right key bias, negative numbers a left key bias. Linear regressions for the key preference over the 30 reversal blocks were positive and showed a significant correlation for the right-eye ($y = -0.053 \pm 0.015 x; r = 0.812; P < 0.001$) and left-eye seeing group ($y = 0.025 \pm 0.017 x; r = 0.846; P < 0.001$). After transfer the group shifted from the right to the left eye still had a right response key bias with a strong correlation between preference scores and number of reversal blocks ($y = 0.211 \pm 0.059 x; r = 0.802; P = 0.005$). The left to right eye group preferred the left response key after the transfer but showed no significant correlation ($y = -0.073 - 0.053 x; r = -0.512; P = 0.130$)

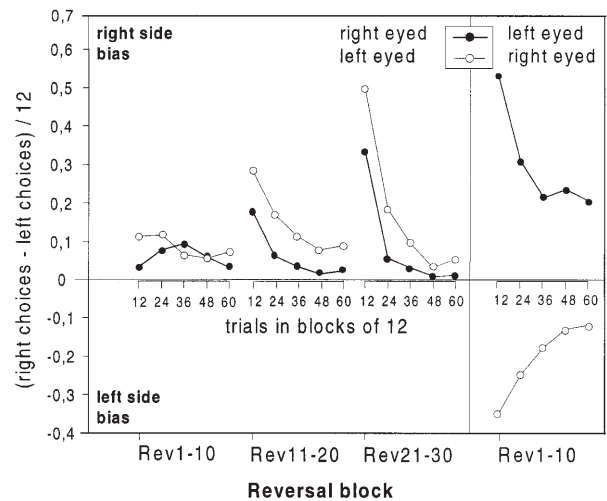


Fig. 7 Inter-session effect on positional bias. Within each reversal session the position bias was calculated for blocks of 12 trials, i.e. 5 blocks of 12 trials within a session consisting of 60 trials. Data were further pooled over blocks of 10 reversals

during the first 12 trials within each session ($t_{29} = 4.56, P < 0.001$; t -test for dependent samples). Similarly the average bias over all trials for the left eye seeing birds was 0.13 ± 0.02 and during the 12 trials at the beginning of each session 0.29 ± 0.07 ($t_{29} = 6.49, P < 0.001$). This change in response bias within a session was very obvious after calculation of the bias values for all blocks of 12 tri-

als, i.e. five blocks within each session of 60 trials (Fig. 7). Whereas bias values were high at the beginning of a session, they continuously decreased and dropped to values below 0.1 at the end of each session. In addition to the robust right side preference at the beginning of each session, this bias also developed as a strategy over the course of repeated reversals. During the first ten reversal blocks almost no bias was noticeable, but during later reversals the response bias at the beginning of a session became very prominent. For the left and right eye group it was about 0.2–0.3 during the first 12 trials during reversals 10–20 and increased to values of about 0.3 for the right-eye-seeing birds, and about 0.5 for the left eye seeing birds during later reversals. A bias of 0.33 and 0.50 was obtained if pigeons pecked the right response key in 8 out of 12 and 9 out of 12 choices, respectively. In all reversal sessions, the bias dropped to values < 0.1 at the end of a session. There was a strong correlation between the reversal number and the magnitude of the response bias as indicated by the correlation coefficients (Fig. 6) for the right-eye-seeing birds ($r = 0.812$; $t_{29} = 7.36$, $P < 0.001$) and the left-eye-seeing birds ($r = 0.846$, $t_{29} = 8.43$, $P < 0.001$). A preference for the right side was preserved by the group that was switched from the right to left eye condition ($r = 0.802$; $t_9 = 3.79$, $P = 0.005$), whereas the other group switching from left to right eye condition showed a preference for the left key ($r = -0.512$; $t_9 = -1.68$, $P = 0.130$). This data pattern reveals that side preferences developed increasingly over the course of the experiment and were clearly related to the eyecap condition in use.

Discussion

The main finding of the present experiment is a superiority of the pigeon's right eye/left hemisphere system in serial reversal learning that was not present during initial acquisition. In addition, there was a difference between the groups with regard to performance before and after change of eyecap condition. Furthermore, both groups showed a response bias towards the right of two response keys during serial reversal learning. This response bias transferred asymmetrically after eyecaps had been switched.

Lateralization during serial reversals

Similar performance of the right eye and left eye system during initial acquisition of the color discrimination indicates that both brain hemispheres are equally competent in establishing this discrimination. As the performance was slightly, though not significantly, better with the right eye, it cannot be ruled out that a bottom effect contributed to equality in performance. A right eye/left hemisphere dominance in visual two-choice discrimination tasks involving brightness, color, simple patterns or objects as relevant cues has been reported in several other studies

(Güntürkün 1985; Mench and Andrew 1986; Vallortigara 1989; Vallortigara et al. 1996; Alonso 1998) but the magnitude of the superiority depends on the specifics of the stimuli or the behavioral paradigm. In any case, results of this study suggest that the specific demands of learning the simple simultaneous color discrimination may not require an outright lateralization of visual processing.

In contrast, lateralization emerged in the course of serial reversal learning. During the first reversal session both groups accumulated a very high number of errors with no significant difference in performance. But a robust asymmetry became evident over the series of 30 reversals. Birds using their right eye performed at a significantly higher level of accuracy than those using their left eye as indicated by the significant group effect of the 2*3 ANOVA. In addition, the variable c of the exponential functions to the learning curves that describes the learning-to-learn effect in mathematical terms assumed significantly different values for the two groups. Birds learning with their right eye/left hemisphere system improved faster than those depending on their left eye/right hemisphere system. This supports the hypothesis that cerebral asymmetries are related to specific demands of surplus cognitive processes involving additional or separate sets of neuronal structures. A clear lateralization in reversal learning as compared to the absence of a strong asymmetry in acquisition might be accounted for by an increase in task complexity. Different levels of task complexity are evident from the fact that the number of trials which were on average needed to master the different aspects of the task increased from about 100 for acquisition ($\cong 1.9$ sessions) of the color discrimination to about 200 for the first reversal learning ($\cong 3.3$ sessions) to about 800 ($\cong 13.4$ sessions) until a 'learning-to-learn' effect could reliably be observed for serial reversals. Because trial number is an indicator for task complexity and the achievement of each step is a prerequisite for the next, the different aspects of the task are likely related to different processing levels related to specific cognitive demands.

Interestingly, as in humans (Teng 1998) one brain hemisphere is primarily in charge of these additional requirements. It is not yet clear exactly which are the processes specific to serial reversal performance. Based on the present results, two kinds of cognitive processes are likely candidates, attentional mechanisms and superordinate mechanisms controlling response strategies. Serial reversal learning requires the subjects to reverse contingencies between a certain stimulus and the related reward expectancy, but to maintain and even increase the attention to the relevant stimulus dimension. Furthermore, a key to the pigeons' improvement during serial reversal learning was that they learned to skip the perseveration stage of reversal learning and to start each reversal with a position habit (see below). Thus, lateralized brain mechanisms which led to better performance with the right eye might be a higher-order cognitive process that controls to what stimulus dimension a subject attends and which response strategy it chooses. Actually, both options could represent two sides of the same coin since a position habit can

be conceived of as one of several hypotheses (Krechevsky 1932) about the relevant stimulus dimension.

Reversal learning has repeatedly been shown to be affected by lesions of the ascending thalamofugal (Macphail 1971, 1975, 1976; Shimizu and Hodos 1989) and tectofugal pathways (Chaves et al. 1993; Chaves and Hodos 1998). The effects of tectofugal lesions on color reversal learning have been shown to be more profound than thalamofugal ones (Chaves et al. 1993). Additionally, it is possible that thalamofugal lesions exert their effects via their projections to the tectofugal system (Chaves and Hodos 1998). Since the tectofugal system displays morphological (Güntürkün 1997c) and connectional asymmetries (Güntürkün et al. 1998), and since tectofugal lesions affect visual discrimination in a lateralized way (Güntürkün and Hahmann 1999), lateralized overall performance in reversal learning as observed in the present study could possibly result from asymmetries of tectofugal mechanisms.

Interhemispheric transfer

At first sight, the finding of a significant difference between pre- and post-shift performance in birds that switched from the right to the left eye but not vice versa appears to match quite well findings of a unilateral transfer from left eye to right eye system and unilateral memory stores in other birds. Food-storing birds remembering cache sites for 24 h hold locations in memory in their left hemisphere independent of the eye or hemisphere used during caching (Clayton 1993; Clayton and Krebs 1994). Similarly in chicks, categorical memory acquired with the left eye/right hemisphere is transferred to the left hemisphere within 24 h (Anokhin and Tiunova 1996). We feel, however, that in terms of interocular transfer the present findings should be interpreted with caution. A detailed analysis of post-transfer scores should also take into consideration that asymptotic error scores during pre-transfer reversals 21–30 are likely to represent different maximum performance levels, i.e. stable asymmetries in the performance of the left and right eye systems. Compared to this level showing each hemisphere at its best, both groups evinced an increase in the number of errors (see Fig. 3). This drop in performance is about 7.9% based on the means of the two groups, i.e. the mean pre-transfer performance of 13.4% $[(11.8 + 15.0)/2]$ and post-transfer performance of 21.3% $[(22.3 + 20.3)/2]$. Both groups encountered difficulties when starting to perform the task with the untrained eye/hemisphere, thus, the interocular transfer was not perfect. Moreover, pigeons tested with their right eye accumulated fewer errors before transfer than those tested monocularly left, which accounts for the 3.2% difference in performance (11.8% vs 15.0%). Given no asymmetries in transfer, both groups of monocularly tested pigeons should have error levels that are elevated by the same amount but adjusted by the right eye advantage. Accordingly, the right-eye-trained birds starting at 11.8% errors should have had an increased error rate of

19.7% due to incomplete transfer (+7.9%) and even higher of 22.9% errors due to the fact that they were now performing the task with the subdominant left eye (+3.2%). In contrast, the error rate of left-eye-trained birds shifted to the right eye was expected to be about 19.7% $[15.0 + 7.9$ (incomplete transfer) -3.2 (right eye advantage)]. The observed error rates after interocular transfer matched the expected values almost perfectly (right eye: observed 22.3%, expected, 22.9%; left to right eye: observed 20.3%, expected 19.7%). In summary, it is not likely that our data reflect asymmetries in interocular transfer of the reversal task. They also suggest that one should take into account asymmetries that are evident prior to the transfer when interpreting interocular transfer data that show differences in the pre- versus post-transfer performance.

Side preferences as a strategy

Instead of being a handicap for successful reversal learning, side preferences might be a useful strategy to accumulate sufficient and reliable information about the reinforcement contingencies in a serial reversal task. Because the negative and the positive stimulus were randomly positioned but presented equally often within 12 trials according to a random sequence by Fellows (1967), the position habit cannot be due to an imbalance in stimulus occurrence. Instead of a gradual decline over time, the response bias in our study became even stronger as shown by the positive correlation between the number of completed reversal blocks and the bias values. Although position habits were often seen as an intermediate ‘chance’ stage (Stettner 1974) without recognizing their cognitive value, position preferences are more likely to be a highly rewarding cognitive strategy. While the animals receive no reinforcement during initial perseveration, their reinforcement rate immediately increases to 50% after choosing to respond to one side only. During the chance stage relevant cues are reduced to only the color variable, as position is fixed, and birds can focus their attention exclusively on establishing new reward contingencies. This cognitive strategy probably helps to quickly improve performance so that an intermediate testing state of stimulus-reward contingencies may be minimized to the initial trials of each session, which reduces error rates on the long term. Although several groups do not report a position bias, perhaps because they did not formally investigate this point (Chaves et al. 1993; Chaves and Hodos 1997, 1998), a general position preference during color discrimination and reversal learning was reported by others (Shimizu and Hodos 1989; Vallortigara 1989).

If the employment of a position strategy was part of the reason the pigeons in the present study could successfully minimize their error rates, it should be especially useful at the beginning of the sessions, when animals had no clear knowledge of the current contingencies. A stronger bias was indeed observed at the beginning of each session. The application of this behavioral strategy was also evident after switching eyecaps. The increase in the strength of the

response key preference at the beginning of each of the ten post-transfer reversals paralleled improvements in overall performance, which inevitably lowered the overall response bias. However, there were some striking differences in the post-transfer behavior. The position bias obvious at the beginning of each session developed much faster and reached values of up to about 0.85 (11 : 1). This might be attributable to the fact that the birds had already acquired this behavioral strategy in previous reversal sessions but after switching eyecaps exploited it successfully to reduce overall error levels rapidly.

Direction of position biases

Whereas the occurrence of a position strategy per se can thus be accounted for straightforwardly, several factors could have contributed to the highly biased direction of the position preferences that emerged in the course of repeated reversals. Taken together they should account for the direction of the position bias, a stronger bias for pigeons using their left eye than those using their right eye, an increase in the strength of the position preference and the asymmetrical shift after interocular transfer.

The first factor, a persistent bias for the right response key, reflects a preference that is related to the visual dominance of the right eye in visual discrimination tasks. Accordingly, birds experimentally naive to the reversal task might have preferred the right response key which then determined the direction of the emerging position strategy. A similar observation was made by Vallortigara et al. (1996) in domestic chicks. This would explain the right position bias independent of the monocular testing condition.

The second proposed variable is dependent on learning and thus changes with the experience of the animals. We suppose that it reflects a strategy of the animals to scrutinize both keys simultaneously with the uncovered eye to reduce errors in choosing the correct color. If pigeons wearing eyecaps try to see both keys simultaneously, they have to turn their head in the direction of the eyecap. Pigeons seeing with their right eye should thus turn their head to the left, while the opposite would apply to pigeons tested with their left eye. Such a head position would bring their beak closer to the key position on the left or right side, respectively, and should increase pecks to the side of the eyecap. If this eyecap-based position preference is also influenced by a left hemisphere dominance, birds using their left eye should develop a stronger bias to the right side since both factors are additive in these animals. Conversely, in birds using their right eye the two variables would have conflicting values (left hemisphere dominance = right side bias; eye cap on the left = left side bias) resulting in reduced overall sidedness.

Although this scenario is able to explain the data set prior to interocular transfer, it is seriously challenged by the results thereafter. However, it is conceivable that the sessions before and after transfer were treated very differently by the animals. Experimentally naive birds might

have preferred the right response key, largely independent of the side of the covered eye, because of the left hemisphere dominance during acquisition which then determined the direction of the emerging, learning dependent side preference. On the other hand, experienced birds might have relied more strongly on the strategy of simultaneous key-viewing. Thus, after switching of the eyecaps birds using their right eye should have preferred the left key whereas those using their left eye should have preferred the right response key. This would explain why, once established, the direction of the position bias could only be reversed when the bird was challenged by a new experimental condition, i.e. switching of eyecaps, which required a shift in head-turning direction in birds switched from the left to the right eye but not vice versa.

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References

- Alonso Y (1998) Lateralization of visual guided behaviour during feeding in zebra finches (*Taeniopygia guttata*). *Behav Proc* 43: 257–263
- Andrew RJ (1983) Lateralization of emotional and cognitive function in higher vertebrates, with special reference to the domestic chick. In: Ewert JP, Capranica RR, Ingle DJ (eds) *Advances in vertebrate neuroethology*. Plenum Press, New York, pp 477–510
- Andrew RJ (1991) The nature of behavioural lateralization in the chick. In: Andrew RJ (ed) *Neural and behavioural plasticity*. Oxford University Press, Oxford, pp 536–554
- Anokhin KV, Tiunova AA (1996) Interocular transfer of experience in forming categorical memory in chickens. *Dokl Akad Nauk* 348: 564–566
- Benowitz L, Lee Teng E (1973) Contrasting effect of three fore-brain ablations on discrimination learning and reversal in chicks. *J Comp Physiol Psychol* 84: 391–397
- Bischof HJ, Watanabe S (1997) On the structure and function of the tectofugal visual pathway in laterally eyed birds. *Eur J Morphol* 35: 246–254
- Catania AS (1965) Interocular transfer of discriminations in the pigeon. *J Exp Anal Behav* 8: 147–155
- Chaves LM, Hodos W (1997) Hyperstriatum ventrale in pigeons: effects of lesions on color-discrimination and color-reversal learning. *Vis Neurosci* 14: 1029–1041
- Chaves LM, Hodos W (1998) Color reversal-learning deficits after tectofugal pathway lesions in the pigeon telencephalon. *Behav Brain Res* 90: 1–12
- Chaves LM, Hodos W, Güntürkün O (1993) Color-reversal learning: effects after lesions of thalamic visual structures in pigeons. *Vis Neurosci* 10: 1099–1107
- Clayton N (1993) Lateralization and unilateral transfer of spatial memory in marsh tits. *J Comp Physiol A* 171: 799–806
- Clayton NS, Krebs JR (1994) Lateralization and unilateral memory transfer in marsh tits: are two eyes better than one? *J Comp Physiol A* 174: 769–773
- Davey G (1989) Learning and intelligence. In: Davey G (ed) *Ecological learning theory*. Routledge, London, pp 274–308

- Deng C, Rogers LJ (1997) Differential contributions of the two visual pathways to functional lateralization in chicks. *Behav Brain Res* 87:173–182
- Fellows BJ (1967) Chance stimulus sequences for discrimination tasks. *Psychol Bull* 67:87–92
- Gaston KE, Gaston MG (1984) Unilateral memory after binocular discrimination training: left hemisphere dominance in the chick? *Brain Res* 303:190–193
- Gossette RL, Gossette MF, Riddell W (1966) Comparisons of successive discrimination reversal performances among closely and remotely related avian species. *Anim Behav* 14:560–564
- Green L, Brecha N, Gazzaniga MS (1978). Interocular transfer of simultaneous but not successive discriminations in the pigeon. *Anim Learn Behav* 6:261–264
- Güntürkün O (1985) Lateralization of visually controlled behavior in pigeons. *Physiol Behav* 34:575–57
- Güntürkün O (1997a) Avian visual lateralization: a review. *Neuroreport* 8(6): iii–xi
- Güntürkün O (1997b) Visual lateralization in birds: from neurotrophins to cognition? *Eur J Morphol* 35:290–302
- Güntürkün O (1997c) Morphological asymmetries of the tectum opticum in the pigeon. *Exp Brain Res* 116:561–566
- Güntürkün O, Hahmann U (1994) Cerebral asymmetries and visual acuity in pigeons. *Behav Brain Res* 60:171–175
- Güntürkün O, Hahmann U (1999) Functional subdivisions of the ascending visual pathway in the pigeon. *Behav Brain Res* 98:193–201
- Güntürkün O, Kesch S (1987) Visual lateralization during feeding in pigeons. *Behav Neurosci* 101:433–435
- Güntürkün O, Melsbach G, Horster W, Daniel S (1993) Different sets of afferents are demonstrated by the fluorescent tracers fast blue and rhodamine. *J Neurosci Methods* 49:103–111
- Güntürkün O, Hellmann B, Melsbach G, Prior H (1998) Asymmetries of representation in the visual system of pigeons. *Neuroreport* 9:4127–4130
- Hambley JW, Rogers LJ (1979) Retarded learning induced by intercerebral administration of amino acids in the neonatal chick. *Neuroscience* 4:677–684
- Horn G, McCabe BJ, Cipolla-Neto J (1982) Imprinting in the domestic chick: The role of each side of the hyperstriatum ventrale in acquisition and retention. *J Exp Brain Res* 53:91–98
- Krechevsky I (1932) Hypotheses in rats. *Psychol Rev* 39:516–532
- Mackintosh NJ, Wilson B, Boakes RA (1985) Differences in the mechanisms of intelligence among vertebrates. In: Weiskrantz L (ed). *Animal intelligence*. Clarendon Press, Oxford, pp 53–66
- Macphail EM (1971) Hyperstriatal lesions in pigeons: effects on response inhibition, behavioral contrast, and reversal learning. *J Comp Physiol Psychol* 75:500–507
- Macphail EM (1975) Hyperstriatal function in the pigeon: response inhibition or response shift? *J Comp Physiol Psychol* 19:607–618
- Macphail EM (1976) Evidence against the response-shift account of hyperstriatal function in the pigeon (*Columba livia*). *J Comp Physiol Psychol* 90:547–559
- Martinoya C, Le Houezec J, Bloch S (1988) Depth resolution in the pigeon. *J Comp Physiol A* 163:33–42
- Mello NK (1968) Interhemispheric transfer of a discrimination of moving patterns in pigeon. *Brain Res* 7:390–398
- Mench JA, Andrew RJ (1986) Lateralization of a food search task in the domestic chick. *Behav Neural Biol* 46:107–114
- Remy M, Emmerton J (1991) Directional dependence of intraocular transfer of stimulus detection in pigeons (*Columba livia*). *Behav Neurosci* 105:647–652
- Remy M, Watanabe S (1993) Two eyes and one world: Studies of interocular and intraocular transfer in birds. In: Zeigler HP, Bischof HJ (eds.). *Vision, Brain, and Behavior in Birds*. MIT Press, Cambridge, Mass, pp 323–350
- Rogers LJ (1995) The development of brain and behavior in the chicken. CAB International, Wallingford
- Rogers LJ, Anson JM (1979) Lateralization of function in the chicken forebrain. *Pharmacol Biochem Behav* 9:735–740
- Rose SP (1991) How chicks make memories: the cellular cascade from c-fos to dendritic remodelling. *Trends Neurosci* 14:390–397
- Shimizu T, Hodos W (1989) Reversal learning in pigeons: Effects of selective lesions of the Wulst. *Behav Neurosci* 103:262–272
- Stettner LJ (1974) The Neural Basis of Avian Discrimination and Reversal Learning. In: Goodman IJ, Schein MW (eds) *Birds: brain and behavior*. Academic Press, New York, pp 165–202
- Teng EL (1998) Hemispheric differences in serial reversal learning: a study with commissurotomy patients. *Neuropsychologia* 36:1025–1032
- Vallortigara G (1989) Behavioral asymmetries in visual learning of young chickens. *Physiol Behav* 45:797–800
- Vallortigara G, Andrew RJ (1994) Differential involvement of right and left hemisphere in individual recognition in the domestic chick. *Behav Proc* 33:41–58
- Vallortigara G, Regolin L, Bortolomioli G, Tommasi L (1996) Lateral asymmetries due to preferences in eye use during visual discrimination learning in chicks. *Behav Brain Res* 74:135–143
- Von Fersen L, Güntürkün O (1990) Visual memory lateralization in pigeons. *Neuropsychologia* 28:1–7
- Watanabe S, Weiss S (1984) A lack of interocular transfer of spatial conditional discrimination in pigeons. *Behav Brain Res* 12:65–68
- Weidner C, Repérant J, Miceli D, Haby M, Rio JP (1985) An anatomical study of ipsilateral retinal projections in the quail using radioautographic, horseradish peroxidase, fluorescence and degeneration techniques. *Brain Res* 340:99–108