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Reverse lateralization of visual discriminative abilities in the European starling

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Previous experiments on visual feature discrimination abilities have consistently shown a right-eye system lateralization in pigeons, *Columba livia*, and young domestic chickens, *Gallus gallus domesticus*, both nonpasserine species. Recently, however, it has been shown that photoreceptor distribution in the left and right retinas are asymmetrical in the European starling, *Sturnus vulgaris*, a passerine species. Single cone receptors are significantly more abundant in the left retina, which suggests that starlings should perform visual discrimination tasks more proficiently with the left eye, in contrast to previous findings with nonpasserines. We tested this hypothesis using the technique of monocular occlusion. In the first experiment, starlings were tested on a simultaneous visual discrimination task in three conditions: binocular (both eyes), left monocular (left eye only) and right monocular (right eye only). Subjects in the binocular and left-monocular conditions achieved significantly higher performance scores on the discrimination task than birds in the right-monocular condition. A second experiment found similar results, with birds in the left-monocular condition learning the discrimination task more than twice as quickly as those in the right-monocular condition. Subsequent tests with the alternative eye for both groups indicated no interocular transfer. These findings suggest that visual discriminative abilities in starlings are asymmetrical, and that they are lateralized in the opposite eye system than has been reported for all other species tested to date.

Lateralization or asymmetry of visual function is a well-known phenomenon in birds (Rogers 1980; Bradshaw & Rogers 1993; Güntürkün 1997). This is due at least in part to the fact that there is almost complete crossover of the optic nerves in the optic chiasm of the avian brain (Cowan et al. 1961; Weidner et al. 1985). In addition, the avian brain lacks a corpus callosum, a brain structure in mammals that connects and allows communication between the two brain hemispheres. In birds, only a few fibres have been found to connect the two hemispheres (e.g. Saleh & Ehrlich 1984); therefore, the contralateral hemisphere receives almost all the visual stimuli entering an eye.

This eye–brain system has allowed researchers to examine the lateralization of a variety of different visual and cognitive abilities in birds, including vigilance (Rattenborg et al. 1999; Franklin & Lima 2001), imprinting (Horn et al. 1983; Vallortigara & Andrew 1991), spatial memory (Vallortigara et al. 1988; Clayton 1993) and visual feature discriminations (Gaston & Gaston 1984; Andrew 1988; von Fersen & Güntürkün 1990). Previous monocular occlusion experiments using visual discrimination tasks have consistently shown a right-eye system lateralization (Bradshaw & Rogers 1993; Güntürkün 1997). Such asymmetry has been shown to enhance discrimination success, possibly due to a reduced conflict between the two hemispheres (Güntürkün et al. 2000). Surprisingly, however, virtually all studies explicitly investigating the lateralization of visual discriminative abilities have used only two orders of nonpasserine species: Galliformes, specifically domestic chickens, *Gallus gallus domesticus* (Rogers 1980; Mench & Andrew 1986; Andrew & Dharmaretnam 1993), and Columbiformes, specifically rock doves, *Columba livia* (Gaston & Gaston 1984; Güntürkün 1985; Güntürkün & Kesch 1987; von Fersen & Güntürkün 1990; Güntürkün et al. 2000).

Recently, Hart et al. (2000) reported morphological asymmetries at the level of the retina in the European starling, *Sturnus vulgaris*, a passerine (songbird) species. They found that all types of single cone photoreceptor cells (short-, medium- and long-wavelength-sensitive)

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were more abundant in the left eye relative to the right eye, and that the opposite was true for long-wavelength-sensitive double cones (Hart et al. 2000). This has interesting implications because it suggests that the left eye should be better at performing discrimination tasks than the right eye (Hart et al. 2000), which is in contrast to previous findings with all other avian species tested to date.

We sought to determine whether visual discriminative abilities are indeed lateralized in the starling, a species that has been shown to perform well on simultaneous discrimination tasks (Templeton 1998). If so, and if the differences at the level of the retina do indeed influence visual discrimination abilities (Hart et al. 2000), then we would expect starlings to be better at learning a visual discrimination task with the left eye than with the right. If, however, visual discriminative abilities are lateralized in the right eye system in starlings as has been found in other birds, then we might expect the right eye to achieve better acquisition scores.

EXPERIMENT 1

Methods

Subjects and apparatus

Twelve wild-caught adult starlings (six males and six females) that had been in captivity for at least 2 weeks were used as subjects. Two additional birds did not complete experimental trials because they attempted to remove their eye rings (see below). All birds were housed in individual cages (46 × 60 × 40 cm) on a 12:12 h light: dark cycle. Birds were provided with water ad libitum and maintained at approximately 85–90% of their free-feeding weight during the experimental trials by depriving them of food for 5 h before each experimental session and by allowing them to feed for 5 h after each experimental session. Birds were fed a combination of breadcrumbs, egg layer crumbles, fruit pellets and Hagen insectivorous mix. All birds received at least 2 days of free feeding before their release at the point of capture.

During all training and experimental trials, individual subjects were placed in a hardware cloth test cage (30 × 30 × 30 cm). The cage had a small opening (4 × 3 cm) through which the subject's head could reach the food wells. The apparatus consisted of two inverted petri dish lids (1 cm high, 3.5 cm diameter) that were placed over food wells (1.7 cm deep, 2 cm diameter) set 3.5 cm apart in a block of wood (13.5 × 8.7 × 2 cm). To make the petri dish lids more difficult to push off the wells, weights (18.6 g) were taped to the inside of the lids. The two test lids presented during experimental trials had unique black and white patterns.

Training and testing trials

During training trials, subjects were presented with a white petri dish lid covering a single food well in a block of wood (11 × 8.7 × 2 cm). Birds were trained by successive approximations (shaping) to peck at a single white petri dish lid (18.6 g) to obtain the hidden food reward (half a mealworm, *Tenebrio molitor*). During training trials, birds had Nexcare 3M Spot Band-Aid rings glued around their eyes with Eyelure cosmetic eyelash glue. The spot band-aids were cut to 1.5 cm in diameter and had the centre removed (0.75 cm diameter). Eye rings were removed with water prior to release. This procedure was approved by the Institutional Animal Care and Use Committee of Franklin & Marshall College (Protocol No. 2000-05), and adhered to the *Guidelines for the Use of Animals in Research*.

After subjects had achieved the training criterion of pecking off the lid within 20 s, they were presented once with two unrewarded test lids, each with a different black and white pattern or 'icon' (Fig. 1). The chosen icon was recorded and the nonselected icon was designated as the 'correct' lid to be rewarded in the experimental trials, which began the next day. This was done to avoid any pre-existing preference for a particular lid pattern.

Subjects were divided into three treatment groups with four birds (two males, two females) arbitrarily assigned to each: right monocular (left eye covered), left monocular (right eye covered) and binocular (eye rings only). Unlike previous studies, birds in all three groups had eye rings glued around both eyes to control for the presence of the rings and also to impair the binocular field of the open eye and thus minimize the possibility of interocular transfer (Goodale & Graves 1982; Remy & Watanabe 1993). In monocular occlusion trials, an additional ring of Velcro (1.5 cm diameter) with the centre (0.75 cm diameter) removed was glued to either the left or right eye ring, depending on the experimental treatment. The complementary Velcro cap (1.5 cm diameter, with the soft centre cleared) was attached to the matching Velcro ring to impair vision for the monocular occlusion trials. The Velcro eye caps were removed at the end of each daily trial session.

Subjects were placed in the testing cage 10 min before each trial session. The position of the rewarded icon (left or right) for each trial was determined semirandomly with the constraint that the rewarded icon occurred on the same side for no more than two consecutive trials. The icons occurred on each side an equal number of times for each subject. A trial consisted of sliding the test block into position in front of the subject's cage opening. As soon as the bird pecked a lid and ate the worm (if available), the lids were removed immediately by pulling a string attached to the test block. Subjects in each treatment group received an average of 20 trials per day for 5 consecutive days for a total of 100 trials. Trials within each daily session had an average intertrial interval (ITI) of 2 min.

During each experimental session, a subject was considered to have a side bias if it selected the same side (either left or right) for six consecutive trials. In these instances, birds were given a correction procedure (e.g.

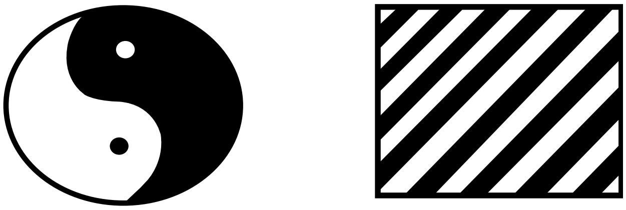

Figure 1. Icons used for simultaneous discrimination task.

Watanabe et al. 1984) in which they received successive presentations of both icons, with the rewarded icon on the nonpreferred side. This was repeated until the bird chose the rewarded side once. A very brief ITI was used during the correction procedure; afterwards, the ITI returned to 2 min. These trials were not included in subsequent analyses.

Subjects were tested until 100 trials had been completed. All trials were recorded with a Sony 8-mm video camera (model no. CCD-TRV15); the observer recording the responses of the birds was blind to the hypothesis and predictions of the study. The performance of each subject was scored as the number of correct responses in each block of 20 trials. All the data collected were included in the analyses except for correction trials used for side biases. Data were analysed using a repeated measures analysis of variance (ANOVAR).

Results

Results of the visual discrimination task are shown in Fig. 2. The ANOVAR showed that there was a significant effect of eye condition ($F_{2,9} = 5.52$, $P = 0.027$) and no significant interaction between condition and trial block ($F_{8,36} = 1.53$, $P = 0.18$). Least squares difference post hoc analyses showed that there was no significant difference in performance between subjects using both eyes (binocular) and subjects using only their left eye ($SE = 1.085$, $P = 0.535$). However, subjects using both eyes performed significantly better than subjects using only their right eye ($SE = 1.085$, $P = 0.024$). Similarly, subjects using only their left eye performed significantly better on the discrimination task than subjects using only their right eye ($SE = 1.085$, $P = 0.008$).

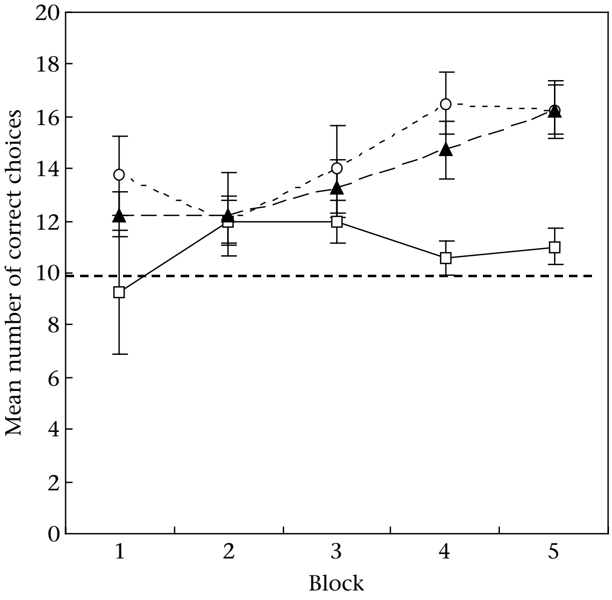

Figure 2. Mean ± SE number of correct choices on the discrimination task made by binocular (▲), right-monocular (□) and left-monocular (○) birds over five 20-trial blocks in experiment 1. Horizontal dashed line represents random choice.

EXPERIMENT 2

Given that our findings in experiment 1 were contrary to those previously found for other avian species, we sought to determine whether these results could be replicated. We made minor changes in the experimental design in an attempt to favour learning of the discrimination task no matter which eye was used, thus making it a more conservative test. We also took advantage of the opportunity to perform interocular transfer tests (e.g. Remy & Watanabe 1993), which had been omitted in experiment 1.

Methods

Subjects and apparatus

Ten wild-caught, adult male starlings in breeding condition were used as subjects. All birds were maintained under the same conditions as described in experiment 1. The apparatus was the same as in experiment 1.

Training and testing trials

The training procedure was the same as in experiment 1, but testing trials differed in several respects. There were only two treatment groups: left eye and right eye. Eye rings and caps were also modified to reduce attempts by the birds to remove the rings. Eye rings consisted of a single ring of cotton string (3 mm thick), glued around each eye with eyelash glue. These were much lighter than those in experiment 1, and did indeed reduce the birds' scratching at the rings. The 'cap' was a circular piece of white cotton glued to the string over either the left or right eye. The ITI was reduced to 1 min to enhance any learning tendencies in both treatment groups. Subjects received an average of 20 trials per day. Trials continued until a learning criterion of nine correct choices in 10 consecutive trials was achieved (e.g. Templeton 1998). Side biases were dealt with in the same manner as in experiment 1; these data were treated separately in subsequent analyses. Interocular transfer tests were performed the day after the learning criterion was reached; thus, the previously occluded eye was uncovered for one full day before testing. These transfer tests consisted of 10 discrimination trials in which the subject's original eye was covered (Remy & Watanabe 1993).

We used a two-tailed *t* test to compare the mean number of trials required to reach the learning criterion in each condition. We used paired *t* tests to compare interocular transfer scores with scores achieved during the first and last 10 test trials in each condition, as well as with random performance (50% correct). We also used *t* tests to analyse side bias data.

Results

Starlings with only their left eye available learned the discrimination task more than twice as quickly as those birds using their right eye (Fig. 3); and despite the small sample size, this difference in performance was significant ($t_6 = 4.891$, $P = 0.0023$). The number of trials required for

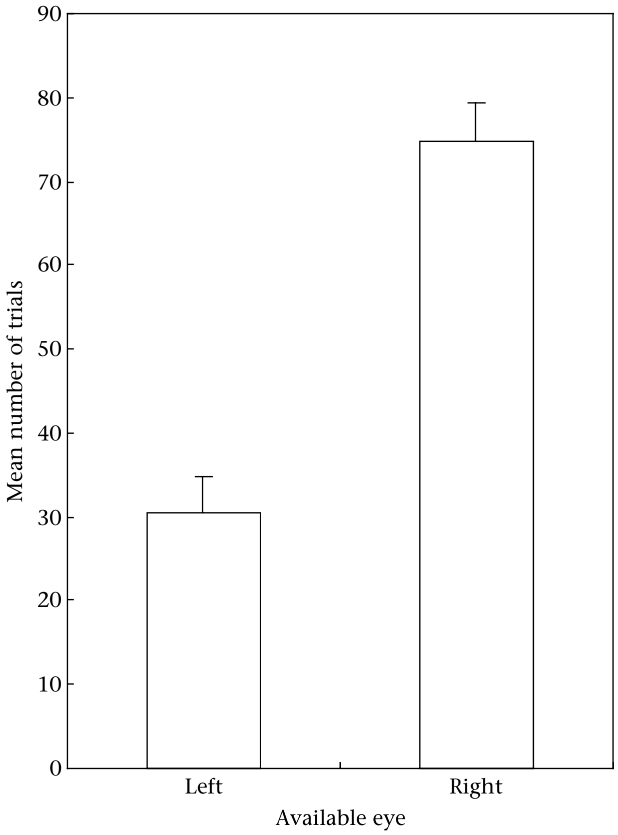

Figure 3. Mean ± SE number of trials required for birds in the left- and right-monocular conditions to reach the learning criterion (nine correct choices in 10 consecutive trials) in experiment 2.

subjects to reach the 90% correct learning criterion ranged from 13 to 37 in the left eye group, and from 49 to 89 in the right eye group. Thus, unlike the birds in experiment 1, birds in the right eye condition did acquire the discrimination task within 100 trials in experiment 2.

Side biases occurred more often in right-eyed birds (4 ± 2.3 times) than in left-eyed birds (1.4 ± 0.9 times), with a significant difference ($t_8 = -2.316$, $P = 0.049$). Left-eyed birds required a mean of 9.8 ± 11.0 remedial trials to remove the bias and right-eyed birds required 20.4 ± 24.5 remedial trials; however, this difference was not significant ($t_8 = -0.881$, $P = 0.404$). Interestingly, the side towards which birds were biased did not appear to be related to their available eye; of the nine birds that developed side biases, five were biased towards the opposite side from their available eye.

Results of the postacquisition transfer tests indicated no apparent interocular transfer (Fig. 4). Birds in both groups performed at levels no different from chance whether the transfer was from the left to right eye ($t_4 = 0.345$, NS) or from the right to left eye ($t_4 = -1.0$, NS). For both groups, this performance was significantly different from the 90% correct choices achieved during the last 10 acquisition trials (left to right: $t_4 = -6.55$, $P < 0.005$; right to left: $t_4 = -21$, $P < 0.001$), but was not significantly different from their performance during the first 10 acquisition trials (left to right: $t_4 = 0$, $P = 1$; right to left: $t_4 = -1.871$, $P = 0.135$).

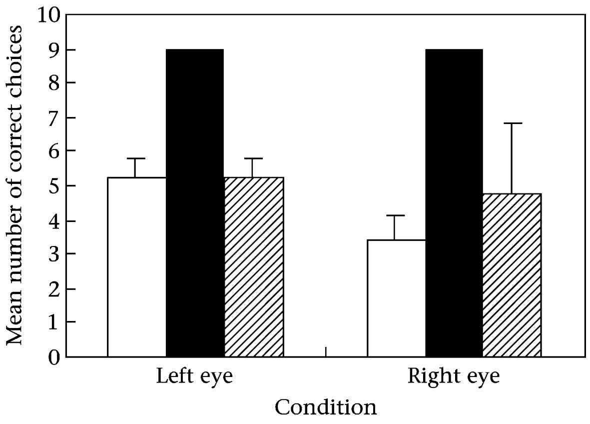

Figure 4. Mean ± SE number of correct choices made by birds in the left- and right-monocular conditions in experiment 2 during the first 10 trials (☐), the last 10 trials (■) and the 10 postacquisition trials with the alternative eye (▨).

DISCUSSION

In both experiments, starlings performed simultaneous visual discrimination tasks more proficiently with the left eye than with the right. In addition, there was no difference in performance between left-monocular and binocular birds in experiment 1, which suggests that even when both eyes were available, the left eye system performed the discrimination (Mench & Andrew 1986; Alonso 1998). These results are contrary to what has been found in pigeons and chickens, which have consistently shown a right-eye system lateralization in their visual discriminative abilities (reviewed by Bradshaw & Rogers 1993; Güntürkün 1997). However, our findings are compatible with the recent finding of retinal asymmetry in starlings (Hart et al. 2000), which predicts better visual discrimination by the left eye.

Birds in the right-monocular condition did not acquire the discrimination at all in experiment 1, and they took much longer to learn the discrimination in experiment 2 than the left-monocular birds. Right-monocular birds were also significantly more likely to develop side biases. Position and colour biases are common phenomena in discrimination experiments when birds do not have access to the relevant information (Templeton 1998; Templeton et al. 1999). In this case, the birds did have access to the information, but were apparently unable to process it properly either because they lacked the appropriate photoreceptor cells in the right retina or because the information was not reaching the potentially more specialized right hemisphere. Thus, a side bias was perhaps an attempt to impose a foraging rule on a more difficult foraging task.

Although right-monocular birds reached the learning criterion more than twice as slowly as left-monocular birds, they did learn the task in experiment 2. This result suggests that the left hemisphere apparently is capable of performing discriminations despite the relatively low frequency of single cone photoreceptors in the right retina (Hart et al. 2000). An alternative explanation, however, is that there perhaps was some interocular transfer of information from the right eye to the ipsilateral hemisphere (Goodale & Graves 1982; Remy & Watanabe 1993) that allowed the right-monocular birds to acquire the discrimination task, albeit with some difficulty. This possibility can be ruled out by the results of the interocular transfer test, which indicated that there had been no transfer of information to the right hemisphere during the testing period. This finding also suggests that there was no interocular transfer in experiment 1.

A complete lack of interocular transfer was somewhat surprising, given that starling eyes are able to move forward into frontal positions as the beak opens, apparently to allow binocular vision while probing for food (Feare 1984; Martin 1986). However, the starlings were not opening their beaks as they viewed the two stimuli, and the eye rings were specifically designed to block information from reaching the binocular field of the open eye. In addition, the fact that there were only 10 transfer test trials may have precluded the possibility of detecting interocular transfer. Indeed, the slight, albeit nonsignificant, improvement in performance (compared with initial baseline) by the right-eyed birds during the post-test with the left eye suggests that some unilateral transfer of information (from left to right hemisphere) may have occurred (e.g. Clayton 1993).

To date, only one other passerine, the zebra finch, *Taeniopygia guttata*, has been tested specifically for the lateralization of visual discriminative abilities (Alonso 1998). In the ‘pebble floor test’, Alonso (1998) reported that right-eyed birds discriminated between beads and food grains more accurately than left-eyed birds. However, the difference was only detectable near the end of the trial; for the first 30 pecks out of 45, the left-eyed birds were actually more accurate than the right-eyed birds (Alonso 1998) and overall, the left-eyed birds appeared to perform well above chance (12 correct pecks out of 15 on average). It would be worthwhile to test zebra finches on the same simultaneous discrimination task presented here to determine whether they show the same lateralization as pigeons and chickens, or whether they show the reverse lateralization demonstrated for starlings.

Our findings are consistent with an asymmetry at the retinal level (Hart et al. 2000), but they do not rule out the possibility of a reversal in functional lateralization at the cerebral and cognitive levels as well. Further experimentation, such as injecting cyclohexamide (Rogers & Anson 1979) or lesioning (Watanabe 1991) will be required to investigate this possibility. If there is indeed a reversal in the lateralization of visual discriminative abilities in the cerebral hemispheres of the starling brain, how could this have occurred? Developmentally, it might be explained by the well-documented effect in which whatever eye is exposed to light during incubation influences neural development in the tectofugal pathway to the contralateral hemisphere (Freeman & Vince 1974; Rogers 1982; Manns & Güntürkün 1999). To date, only two passerine species ($N = 3$ for each) have been studied during embryonic development (Oppenheim 1972): northern cardinal, *Pyrrhuloxia cardinalis*, and house wren, *Troglodytes aedon*. Both appeared to show the same head position in the egg as has been shown for chickens (head tucked down and turned to the right). But unlike precocial species, eye occlusion is minimal in these altricial species because the head is large relative to the body (Oppenheim 1972). It is unlikely that there is a difference in the position of the embryo in starling eggs compared to other species. However, the reduced eye occlusion, combined with the varied external lighting experienced by these opportunistic cavity nesters might well lead to population differences in asymmetries. For example, one-third of 108 pigeons studied by Güntürkün et al. (2000) displayed a reversed left-eye dominance, although right-eye dominant individuals were significantly more efficient at discrimination tasks.

Although bird song is now known to be under bilateral cerebral control, with peripheral lateralization in only the hypoglossal nucleus and syrinx (McCasland 1987; DeVoogd et al. 1991; Goller & Suthers 1995; Suthers 1997), some hemispheric differences in avian song discrimination have been found (Cynx et al. 1992). Thus, it is tempting to speculate that the reverse lateralization of visual discriminative abilities demonstrated in starlings is a general phenomenon of most passerine species, and that it might be correlated with the neural reorganization that occurred during the evolution of vocal nuclei in the passerine brain (Bradshaw & Rogers 1993; Brenowitz 1997). One way to test this evolutionary hypothesis would be to compare the lateralization of visual discriminative abilities of oscine and suboscine passerines. Like nonpasserines, suboscine passerines completely lack forebrain vocal nuclei (reviewed by Brenowitz 1997). Thus, one might predict that suboscines would show the same right eye asymmetry of visual discriminations shown by nonpasserine species.

Finally, both Hart et al.’s (2000) finding of retinal asymmetry in starlings and the corresponding results of our study have some interesting implications for the ecology of avian vision, particularly with respect to search image formation (reviewed by Pietrewicz & Kamil 1981). As proposed by Rogers (1997) and more recently by Dawkins (2002), birds may use one eye preferentially to search for cryptic prey, or they may learn to detect cryptic prey more rapidly with one eye than with the other. As is clear from the current study, distinguishing retinal limitations from cognitive limitations will likely prove challenging. However, experiments testing for the potential lateralization of the search image in starlings are currently in progress (Christensen 2003).

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