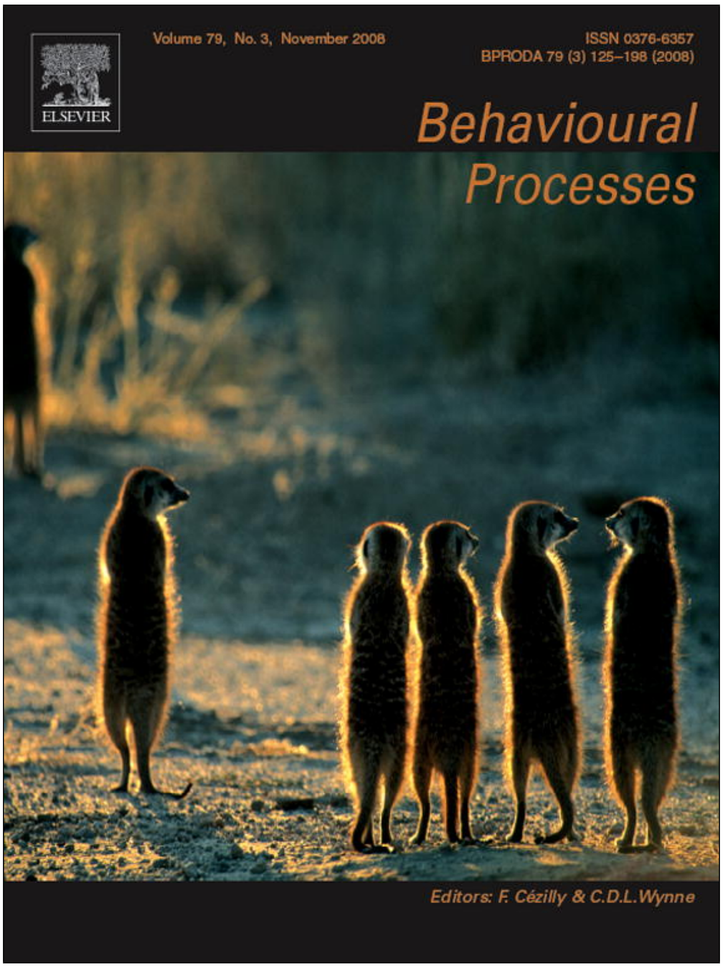
Volume 79, No. 3, November 2008
ISSN 0376-6357
BPRODA 79 (3) 125–198 (2008)
ELSEVIER
Behavioural Processes
Editors: F. Cézilly & C.D.L.Wynne

Behavioural Processes 79 (2008) 125–131

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

A behavioral analysis of prey detection lateralization and unilateral transfer in European starlings (*Sturnus vulgaris*)

J.J. Templeton[a,*], J.M. Christensen-Dykema[b,1]

[a] *Department of Biology, Knox College, Galesburg, IL 61401, USA*
[b] *Department of Psychology, Knox College, Galesburg, IL 61401, USA*

A R T I C L E   I N F O

Article history:
Received 23 September 2007
Received in revised form 20 June 2008
Accepted 24 June 2008

Keywords:
European Starling
Lateralization
Prey detection
Unilateral transfer
Sturnus vulgaris

A B S T R A C T

It has been suggested that birds prefer to use a particular eye while learning to detect cryptic prey and that this eye preference enhances foraging performance. European starlings (*Sturnus vulgaris*) with the left, right, or both eyes available learned to detect inconspicuous cues associated with the presence of hidden prey. Acquisition scores were not significantly different between left and right-eyed birds; however, performance in the binocular condition was significantly higher than in the two monocular conditions. When binocular birds were tested with familiar and unfamiliar cues present simultaneously, the familiar cue was selected significantly more often than the unfamiliar cue, suggesting that the birds were searching for specific cue features. When monocular birds were tested using only the naïve eye, performance dropped significantly. In right-eyed birds using the naïve left eye, performance remained at chance levels over transfer trials. However, left-eyed birds using the naïve right eye had a superior performance compared to the initial acquisition scores of right-eyed birds and also showed a significant improvement in performance over transfer trials. Thus, although there was no direct evidence of lateralization during acquisition, there was unilateral transfer of the prey detection skill from the right to the left hemisphere.

1. Introduction

Functional lateralization is defined as the specialization of one brain hemisphere for a particular task or ability. Avian brain lateralization has been studied extensively for over 30 years, and this is due at least in part to birds' unique brain structure (reviewed by Bradshaw and Rogers, 1993; Rogers, 2002). Birds lack the corpus callosum that transmits information between mammalian hemispheres and there is complete decussation at the optic chiasm; the optic nerve from the left eye transmits all visual information directly to the right hemisphere, and vice versa (Cowan et al., 1961; Weidner et al., 1985). Thus, by using monocular occlusion, it is possible to determine which brain hemisphere is specialized for a particular task. Lateralized visual discrimination skills in particular have been widely studied using this technique (Watanabe et al., 1984; Mench and Andrew, 1986; von Fersen and Güntürkün, 1990; Güntürkün and Kischkel, 1992; Güntürkün and Hahmann, 1994; Alonso, 1998; Templeton and Gonzalez, 2004). To date, most lateralization work on visual discrimination tasks in pigeons (*Columba livia*) and young domestic chickens (*Gallus gallus domesticus*) has found higher performance in the right eye–left hemisphere system (Watanabe et al., 1984; von Fersen and Güntürkün, 1990; Güntürkün and Kischkel, 1992; Güntürkün and Hahmann, 1994). However, Templeton and Gonzalez (2004) recently investigated the lateralization of a visual discrimination task in European starlings (*Sturnus vulgaris*), and found that discrimination skills appear to be lateralized in the left eye–right hemisphere system. This reversal of visual discrimination lateralization may be related to the Hart et al. (2000) finding of an asymmetry of single cone photoreceptor cells in starling retinas.

Recently, Rogers (1997) and Dawkins (2002) have suggested that chickens might attend to particular features of cryptic prey with one eye preferentially over the other in order to search for prey more effectively. If this is the case for starlings as well, then one might expect them to show a lateralization of prey detection abilities similar to that shown for discrimination tasks due to the asymmetry of cone cells. Alternatively, the detection of cryptic or inconspicuous prey might be performed equally well by either eye, but acquisition of the task may be restricted to the learning hemisphere. This has been shown to be the case for spatial memory of food hoarding locations in marsh tits (*Poecile palustris*), at least over the short term (Sherry et al., 1981).

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* Corresponding author.
E-mail addresses: jtemplet@knox.edu (J.J. Templeton), joyce@unlserve.unl.edu (J.M. Christensen-Dykema).
[1] Present address: School of Biological Sciences, University of Nebraska, Lincoln, NE 68588, USA.

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doi:10.1016/j.beproc.2008.06.003

Our study was a preliminary test of these two alternative hypotheses. The first hypothesis predicts that starlings using their left eye should learn to detect prey as well as those using both eyes, and more quickly than those using their right eye. The second hypothesis predicts that subjects using either eye should acquire the task equally quickly, but that their performance should drop when forced to use the naïve eye–brain system.

Starlings learned to search for inconspicuous black cues printed on paper with a black and white background pattern, using either the left or right eye, or both eyes. The cues indicated the location of prey items concealed below the paper; the birds pierced through the paper to access the prey. Alphabet letters and other symbols were used as cues rather than insect-like stimuli because the birds might have recognized the latter too easily as prey, thus eliminating the need to learn to associate a cue with the presence of hidden food. Abstract shapes and symbols have been used in previous prey detection tasks (e.g. Plaisted and Mackintosh, 1995; Blough, 1989), and the use of black and white printed or digital representations is now preferred in such tasks (Bond and Kamil, 1998, 1999, 2002; Blough, 1989) due to the fact that birds are tetrachromats (Robinson, 1994; Vorobyev et al., 1998) and also can detect UV reflectance (Bennett and Cuthill, 1994). Although the cues were not ‘cryptic’ in the sense that they did not blend completely into the background, they were designed to be inconspicuous, and thus difficult to detect. The use of letters and other symbols also allowed us to test whether the birds were simply learning to detect any difference from the background or whether they were learning to search for specific cues.

2. Materials and methods

2.1. Subjects

A total of 22 wild-caught, adult European starlings participated in this experiment. They were housed in a holding room in individual home cages (44 cm × 44 cm × 55 cm) under a 12:12-h light:dark cycle. The birds were given free access to water, and were maintained at approximately 90% of their *ad libitum* feeding weight for the duration of the experiment. *Ad libitum* weight was the weight attained after at least a week in captivity; the birds tended to gain weight in captivity due to the freely available food, warmer temperatures, and reduced activity levels. Thus, 90% of this weight was comparable to their weight at capture. Birds were fed a combination of breadcrumbs, Cargill Inc. chicken layer feed, 8-in-1 softbill fruit pellets, and Hagen insectivorous mix. After trials were completed, birds were again allowed *ad libitum* access to food; they were released once pre-testing weight had been reached.

2.2. Apparatus

Subjects foraged on a “food patch”, a 21.5 cm × 27 cm × 1.8 cm block of wood with 20 holes (2 cm diam) drilled equidistant from each other in a 4 × 5 configuration. Cardboard was glued to the bottom of the patch to hold prey items, and standard (21.5 cm × 26.8 cm) sheets of white, multipurpose recycled paper (Boise, Aspen^{TM}) were taped to the top of the patch using double-sided tape. During training trials, the paper was plain white; during acquisition trials, the paper had a black and white background pattern printed on it (Fig. 1), created using the Paint program in Windows 98 (large airbrush function) and printed on a Xerox Workcentre® Pro 275 with a resolution of 1200 dpi. There also were 20 circles (2 cm diameter) printed directly above the holes of the patch. A cue was printed within six of the 20 circles. Cues were black symbols or letters that ranged in size from 2 to 5 mm in length (Fig. 1). For all trials, a small X was cut into each circle with a razor blade. This facilitated piercing and probing but did not reveal where food was located. Prey consisted of either fresh mealworm halves (*Tenebrio* larvae, Rainbow Mealworms), dehydrated mealworms (“caterpillars”, Audubon Workshop), or small cubes of cheddar cheese or bologna depending on each subject’s preference, which was determined in advance. To provide sufficient footing on the smooth paper, four rubber bands were wrapped around the patch.

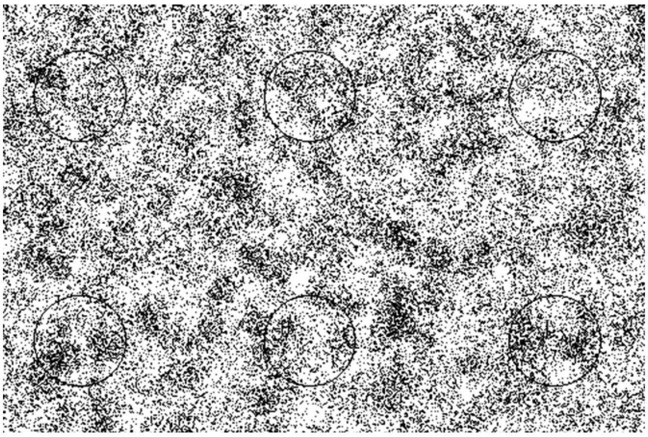

Fig. 1. Section of experimental background showing the six cues in the top left quadrant of each circle. From left to right: triangle Δ; delta ∂; happy face ☺; female symbol ♀, H, and J. Cues were not always in the same locations within the circles. Circles indicated the location of wells.

For the entire duration of the experiment, birds were fitted with eye rings that served two purposes: to keep the eye caps (see below) from touching and irritating the eye, and to prevent the bird from using the binocular fovea in the unoccluded eye (Remy and Watanabe, 1993; Templeton and Gonzalez, 2004). The eye rings consisted of a loop of cotton string, and were adhered to the feathers around both of the bird’s eyes using Andrea® cosmetic eyelash glue. To prevent the birds from scratching the eye rings off, a thin line of eyelash glue was applied to the feathers surrounding the eye ring itself. This made it difficult for the bird’s claws to catch on the cotton string, and was a fairly effective method of retaining eye rings. For each day of test trials, monocular birds were fitted with a temporary eye cap that occluded one eye, thereby blocking direct visual access to the contralateral hemisphere. Eye caps were small ovoid pieces of thin white cotton that were glued to the eye ring. These covers allowed light and air to reach the eye, but vision was effectively blocked. The use of monocular occlusion is a common technique, and it has been reported to give minimal discomfort to most birds (Sherry et al., 1981; Mench and Andrew, 1986; Clayton, 1993). However, two birds did have to be replaced due to their failure to habituate to the eye rings within the required 2-day period.

All training, acquisition, and test trials were conducted in a bird’s home cage in a separate experimental room from the holding room. All types of trial were conducted in a similar fashion: the experimenter pulled out the cage tray, put the food patch in the tray, and replaced the tray. For every training or testing session, a companion bird was present in the room within view of the subject. All companion birds were subsequent subjects in the experiment; however, the companion was placed so that it could not see the experimental patches. The experimenter was hidden from view during each trial.

2.3. Training

For all training sessions, the patch was covered with plain white paper; there was no background pattern or cues, but 20 black circles indicated the location of the wells. Each bird was first "pre-trained" to pierce through the paper to access prey. All 20 wells were baited and additional food was suspended in six random slits so that when the birds pecked at the item, it would disappear into the food well below, eliciting probing. Only one pre-training experience was needed to elicit probing, and training began the following day.

To ensure the bird was willing to check every hole in a patch, prey items were presented randomly in half of the 20 holes; birds were allowed to pierce only 10 holes each training trial. Subjects were trained on this 50% reward patch until they were successfully approaching the patch, probing, and eating within 1 min of presentation. Any side biases apparent in this phase were corrected with non-random prey presentation; we concentrated prey items in (but did not restrict them to) the unfavored sections of the patch until the birds chose at least four holes from this side in two consecutive trials. Once these criteria were met, training was complete.

2.4. Acquisition trials

There were three treatment groups: binocular, with both eyes available (N=6), or monocular, with either the left eye available (N=6), or the right eye available ($N = 6$). Subjects were arbitrarily assigned to one of these groups based on order of capture, completion of training, and sex. There were two males and four females in the binocular and left eye conditions, and three males and three females in the right eye condition. Acquisition of the prey detection task was carried out using the testing background pattern with a cue printed over six holes, selected randomly for each trial using www.random.org (sampling without replacement); prey items were placed in corresponding holes. One subject from each of the three treatment groups was arbitrarily assigned to each of the six different prey cues. We allowed the birds to pierce only six holes in each trial, making maximum possible performance 100%. Daily sessions consisted of 10–20 trials per day until the subject completed 100 trials.

An additional comparison was carried out to test whether the cues used on the patterned background were indeed inconspicuous, and thus difficult to detect. To do this, four naïve binocular birds (two males and two females) were given 100 acquisition trials with cues printed on a plain white background. The four cues used for these birds (♀, H, J, ∂) were selected from the six cues used by the other subjects, and had intermediate conspicuousness scores. The acquisition scores of these four "conspicuous" binocular birds were then compared to the scores of the four "inconspicuous" binocular birds that had used the same cues.

Following acquisition trials, birds in the inconspicuous binocular and monocular conditions were given different types of test trials. These trials started 1 day after acquisition trials were completed.

2.5. Smell control trials and cue probe trials for binocular birds

To test for the possibility that birds were using smell rather than vision to detect prey, binocular birds were given 20 additional trials, five of which were arbitrarily selected to be "control trials". In these control trials, the trained cue was printed over six holes, but all holes were empty and the birds were allowed to pierce only six holes. The next day, to test the hypothesis that the birds were searching for a specific cue rather than any differentiation from the background, binocular birds were given a further 20 trials, five of which were "probe trials". In these probe trials, a total of 12 holes had cues over them: six with the familiar, trained cue, and six with an untrained (novel) cue. Each of the six cues was arbitrarily assigned as a trained cue and as a novel cue in a balanced design over subjects. For example, Bird 1 had the happy face as the familiar cue and the triangle as the novel cue; Bird 2 had the reverse cue designation, and so on. Again, all holes were empty during probe trials, and birds were allowed to pierce only six holes.

2.6. Transfer trials for monocular birds

For monocular birds, eye cap transfer trials followed the completion of acquisition trials in order to test for either restriction of the prey detection task to the learning hemisphere (Sherry et al., 1981), or interocular transfer to the unavailable hemisphere (Remy and Watanabe, 1993). After the last acquisition trial, the eye cap was removed as usual. Transfer tests started the next day after a new cap was affixed over the tested eye. Using the same procedure as in the acquisition phase, birds were tested for 10 more trials with the naïve eye.

2.7. Data analyses

We summarized the data by calculating the mean score for every "block" of 10 consecutive trials for each subject. Ten trials were chosen rather than 20 so that any unusual patterns in performance during daily sessions would not be masked. Thus, in the acquisition phase, there were 10 blocks (100 trials). These data were analyzed using a two-way, repeated-measures ANOVA (ANOVAR) to measure the effect of available eye and block on performance; one-way ANOVARs tested for a change in performance in each eye condition separately. A two-way ANOVAR was used to test the prediction that the cues were indeed difficult to detect by comparing the performance of the inconspicuous and conspicuous binocular conditions over the acquisition period. To determine whether or not performance reached asymptotic stability within 100 trials, each individual bird's performance was analyzed using one-sample Kolmogorov–Smirnoff (K–S) tests.

Paired t-tests compared the performance of binocular birds on food and empty patches during smell control trials. Similarly, paired t-tests compared the binocular birds' responses to familiar and novel cues. For monocular birds, paired t-tests compared performance in the last block of acquisition trials to the eye cap transfer block. The last block and the transfer block were also compared to random performance (1.8 correct choices out of 6) using one-sample t-tests. Finally, a one-way ANOVAR was used to analyze the performance of each naïve eye over the 10 transfer trials. Data were analyzed using SYSTAT (Wilkinson, 1990) and Excel.

3. Results

3.1. Acquisition trials

All subjects completed the 100 acquisition trials (Fig. 2). Performance increased significantly over the 10 blocks of trials in each of the three eye conditions (binocular: $F = 19.213$, d.f. = 9, 45, $p < 0.001$; left: $F = 9.465$, d.f. = 9, 45, $p < 0.001$; right: $F = 7.413$, d.f. = 9, 45, $p < 0.001$). However, binocular birds improved faster than monocular birds, producing a significant block by eye interaction ($F = 2.036$, d.f. = 18, 135, $p = 0.012$). There was no significant difference between left and right eye conditions ($F = 0.005$, d.f. = 1, 10, $p = 0.947$). A one-sample t-test comparing performance in the last block of trials to random (1.8/6 correct) for both the left ($t = 3.853$, d.f. = 9, $p < 0.05$) and right subjects ($t = 3.059$, d.f. = 9, $p < 0.05$) showed that their performance had increased to significantly better than random. Birds in all three eye conditions reached asymptotic performance by block 7 on average; for each subject, score distributions in blocks

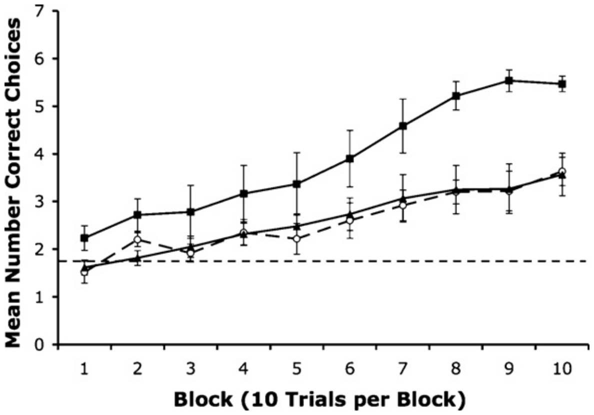

Fig. 2. Mean performance of subjects in all three conditions searching for inconspicuous cues. Closed squares: binocular; open circles: left monocular; closed triangles: right monocular. The dashed line at 1.8 indicates random performance. Error bars represent S.E.

7–10 were not significantly different from each other (K–S tests, $p > 0.05$).

As expected, conspicuous binocular birds performed better than inconspicuous binocular birds (Fig. 3, $F = 4.989$, d.f. = 1, 6, $p = 0.033$, one-tailed test). There was a significant interaction between block and background ($F = 4.324$, d.f. = 9, 54, $p < 0.001$) due to the fact that the birds foraging on conspicuous cues improved their performance much more rapidly than those searching for inconspicuous cues. All conspicuous binocular birds reached asymptotic performance by block 4 on average (K–S tests, $p > 0.05$); this was significantly earlier than for the inconspicuous binocular birds ($t = 2.37$, d.f. = 6, $p = 0.054$).

3.2. *Smell control trials and cue probe trials for binocular birds*

Following acquisition trials, binocular birds were able to detect inconspicuous cues whether food was present or not; the mean number of correct choices did not differ significantly between food (5.68 ± 0.24) and empty (5.75 ± 0.24) trials ($t = -0.531$, d.f. = 5, $p = 0.618$). In probe trials, the binocular birds chose the familiar cue significantly more often than they chose the unfamiliar cue ($t = 4.53$, d.f. = 5, $p = 0.006$) when two different inconspicuous cue types were present simultaneously (Fig. 4). This was significantly different from random choice ($t = 4.58$, d.f. = 5, $p = 0.006$).

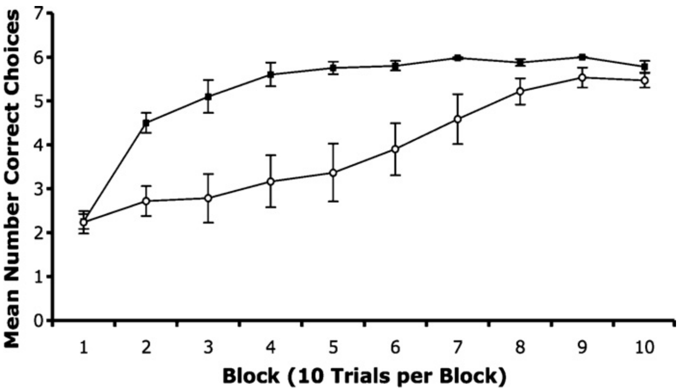

Fig. 3. Mean performance of binocular birds searching for conspicuous and inconspicuous cues. Closed squares: conspicuous. Open circles: inconspicuous. Error bars represent S.E.

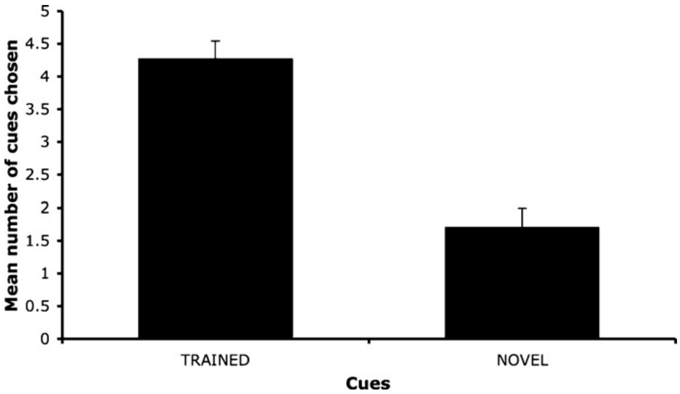

Fig. 4. Mean number of familiar (trained) cues and unfamiliar (novel) cues chosen by binocular birds in the inconspicuous condition. Error bars represent S.E.

3.3. *Eye cap transfer trials for monocular birds*

The results of the eye cap transfer trials are shown in Fig. 5. There was a significant drop in performance for both the right–left birds ($t = 3.83$, d.f. = 5, $p = 0.012$) and the left–right birds ($t = 2.73$, d.f. = 5, $p = 0.042$) when using the naïve eye. The right–left birds' performance was not significantly different from random when using the left eye ($t = -1.28$, d.f. = 5, $p > 0.20$), and it was not significantly different from the performance of left-eyed birds during the initial block of acquisition trials ($t = -1.79$, d.f. = 10, $p = 0.102$; Fig. 2). In contrast, the left–right group's mean performance was still significantly better than random when using the right eye ($t = 5.10$, d.f. = 5, $p < 0.01$; Fig. 5), and it also was significantly higher than the performance of right-eyed birds during the initial block of acquisition trials ($t = -4.54$, d.f. = 10, $p = 0.001$; Fig. 2). Interestingly, although the right–left birds' performance remained at chance levels over the 10 transfer trials ($F = 0.375$, d.f. = 9, 45, $p = 0.941$), the left–right birds showed a gradual, but significant improvement in performance ($F = 2.134$, d.f. = 9, 45, $p = 0.046$; Fig. 6).

4. Discussion

All birds showed a marked improvement in their ability to detect the inconspicuous cues over the 100 trial acquisition period. Binocular birds improved significantly more quickly than monocu-

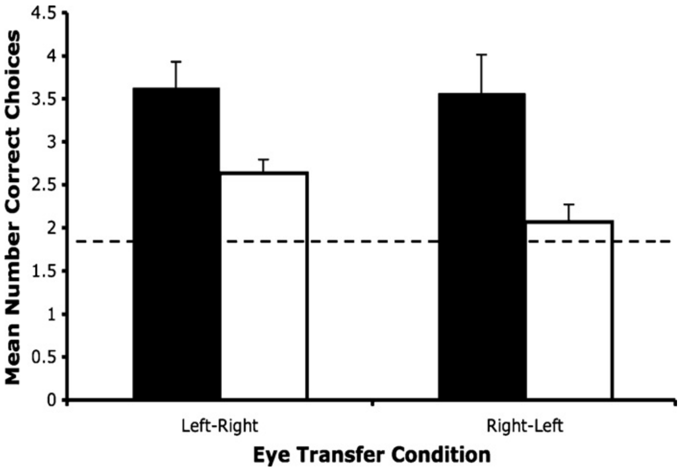

Fig. 5. Mean performance for subjects in left and right eye conditions during block 10 (white) and the transfer block (black). Between the two blocks, the eye cap was transferred to the opposite eye; the naïve eye was tested in the transfer block. Dashed line at 1.8 indicates random performance. Error bars represent S.E.

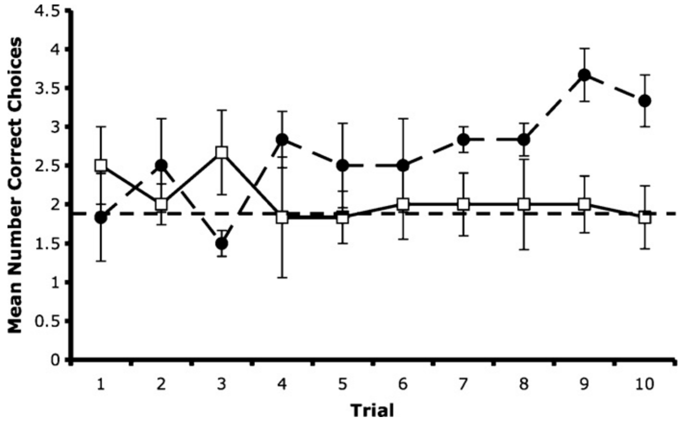

Fig. 6. Mean performance of naïve left and right eyes over 10 transfer trials. Closed circles: left–right; open squares: right–left. Dashed line at 1.8 indicates random performance. Error bars represent S.E.

lar birds, and reached a higher level of asymptotic performance. Subjects using either the left or the right eye were also able to improve cue detection significantly and asymptotically over time, such that performance by the end of trials was significantly better than expected by chance in both conditions. However, there was no significant difference in performance between the two monocular conditions while the birds were learning the task. Thus, we found no evidence for prey detection lateralization during acquisition, which was surprising given Templeton and Gonzalez (2004) finding of lateralization of visual discriminative abilities in the left-eye system in starlings. This implies that visual discrimination tasks and our prey detection task involve quite different cognitive abilities, although they do share some similarities. A simultaneous discrimination task requires that a bird learn to discriminate between two separate and distinctive stimuli and to associate one of these stimuli with hidden food. Similarly, the detection of semi-cryptic prey requires that a bird learn to distinguish between cues and the background and associate the cues with hidden food. How and why these different tasks might affect lateralization differently is, therefore, unclear.

Although not cryptic, the cues were indeed difficult to detect; binocular birds searching for cues printed on a plain, white background acquired the prey detection task significantly more rapidly than binocular birds searching for the same cues printed on the patterned background. Despite the difficulty in detecting cues, however, the fact that all three eye-treatment groups reached asymptotic performance indicates that 100 trials was a sufficient length of time for the acquisition phase of the experiment.

Control trials in which binocular birds searched for inconspicuous cues above empty wells confirmed that the birds were not simply using smell to detect the hidden prey items; subjects selected cues whether prey items were present or not. Most importantly, binocular birds selected the familiar cue significantly more often than they chose the novel cue in probe trials, indicating that they were searching for specific cue features.

Both monocular conditions experienced a significant drop in performance following eye cap transfer, which is consistent with Sherry et al.'s (1981) findings of spatial memory restriction to the learning hemisphere. In right-eyed birds using the naïve left eye, performance remained at chance levels over the 10 transfer trials. This could not be due simply to a lack of practice by the naïve eye, however, because left-eyed birds using the naïve right eye performed significantly better than random and also showed superior performance compared to that of right-eyed birds during initial acquisition trials. They also experienced a significant improvement in performance over transfer trials. Thus, although there was no direct evidence of performance lateralization between the two eyes during acquisition, there was unilateral interocular transfer (Remy and Watanabe, 1993; Clayton, 1993) from the right to the left hemisphere only, and the acquired prey detection skill apparently was restricted to the left hemisphere (Nottelmann et al., 2002).

Interocular transfer can happen when information enters the binocular field and travels via the tectofugal pathway and interhemispheric commissures from the contralateral to the ipsilateral hemisphere (Goodale and Graves, 1982; Remy and Watanabe, 1993; also reviewed by Andrew, 2002). In contrast, visual access to the lateral field alone results in only contralateral information processing (Goodale and Graves, 1982; Goodale, 1985). Similar findings of lateralized interocular transfer of information from the right to the left hemisphere and asymmetrical restriction of information to the left hemisphere have been reported for a food hoarding task in marsh tits, *P. palustris* (Clayton, 1993) and for a conditional discrimination task in pigeons (Nottelmann et al., 2002). In addition, the same transfer direction has been reported for a 'bead floor' task in chickens (Anokhin and Tiunova, 1996). However, the opposite pattern of transfer (from the left to the right hemisphere) has been found for chickens and pigeons (reviewed by Güntürkün, 2002) performing color (Skiba et al., 2000) and pattern (Gaston, 1984; Diekamp et al., 1999) discrimination tasks, as well as in passive avoidance tasks (Rose, 1991; Sandi et al., 1993) and imprinting (Horn, 1991).

One possible explanation for the lower performance of monocular birds during acquisition trials is the fact that the birds were being forced to use the lateral field of view, which has been shown to be 'hypermetropic' (far-sighted) in pigeons and chickens and, thus, not well-equipped to deal with the detection of prey items at close range (Goodale and Graves, 1982; Dawkins, 2002). However, despite our attempts to block the binocular field with eye rings, it is likely that some information did indeed reach this region of the retina. Two pieces of evidence support the possibility that the binocular field was not completely blocked. First, both binocular and monocular birds were able to improve their detection of inconspicuous prey significantly over trials despite the presence of eye rings; and secondly, interocular transfer occurred. It is particularly difficult to block the binocular field in starlings because of their unusual eye morphology. Starling eyes move forward as the beak opens, and there is almost complete binocular overlap when the beak is fully open (Feare, 1984; Martin, 1986). Starlings often open their beaks when looking closely at objects, as they did when searching for cues in this experiment.

It is most likely that the superiority of the binocular condition is simply due to the additive effects of having two eye systems doing exactly same task simultaneously, resulting in a higher probability of detecting the relevant cues. However, an intriguing alternative possibility is that binocular birds performed better than monocular birds because they were better able to integrate differing skills of both hemispheres simultaneously, despite the presence of eye rings (Watanabe et al., 1984). Although there was no difference in the rate of acquisition between left and right eyes, we cannot rule out the possibility that each hemisphere contributes something different to the prey detection task. For example, one hemisphere may be better able to enhance the detection of specific cue features, while the other might function in learning and remembering the association between cues and hidden prey. This latter hypothesis is suggested by our finding of unidirectional interocular transfer from the right to the left hemisphere when left-eyed birds were forced to use the naïve right eye, and by the drop in performance to random when right-eyed birds were forced to use the naïve left eye. This finding implies that the left hemisphere may play a role in long-term memory storage for the prey detection task (Clayton, 1993; Andrew, 2002).

Although the cues used in this experiment were not cryptic, they were certainly difficult to detect. In addition, binocular birds were shown to be searching for specific cue features, rather than simply any differentiation from the background. Thus, our study has important neurological implications for search image formation. The 'search image' is considered to be "a kind of learning process" by which an animal learns the specific characteristics that distinguish a cryptic prey morph from its background (Tinbergen, 1960, p. 316). Although extensive research has been conducted on various alternative explanations for this enhanced perceptual bias (Pietrewicz and Kamil, 1979, 1981; Bond, 1983; Guilford and Dawkins, 1987; Reid and Shettleworth, 1992; Plaisted and Mackintosh, 1995; Langley, 1996; Vreven and Blough, 1998; Dukas and Kamil, 2001), and its consequent effects on prey populations (Bond and Kamil, 1998, 1999, 2002), there are still unanswered questions concerning the phenomenon. The definition of search images that Luuk Tinbergen proposed assumed a neurological change in a predator's brain, although as Tinbergen stated, "as far as we are aware, the nervous mechanism of this [search image] process is not known" (Tinbergen, 1960, p. 332). Is the acquisition of search images lateralized in the avian brain? Is there unilateral transfer or restriction of search image formation to a particular hemisphere? Clearly, our study has shown how future research might begin to take a neuroethological approach to this fascinating ecological phenomenon.

Acknowledgments

This research was in partial fulfillment of the requirements for an Honors degree in Biology for J.M.C. We thank Heather Hoffman, Jim Mountjoy, Tom Valone, Lynne Weber, Ken Yasukawa, Clive Wynne, and four anonymous reviewers for their constructive comments. We are grateful to Sara Fink, Mark Liebich, Mariko Toyoji and Kendra Wright for assisting with data collection. We also thank Elisabeth Brewer, Julian MacDonald, and Miava Reem for their help in caring for the birds during this research. This research was financially supported by the Knox College Richter Fund and NSF Grant IBN 0109024. The research presented here was described in an Animal Research Protocol approved by the Institutional Animal Care and Use Committee (IACUC) of Knox College.

References

Andrew, R.J., 2002. Memory formation and brain lateralization. In: Rogers, L.J., Andrew, R.J. (Eds.), Comparative Vertebrate Lateralization. Cambridge University Press, Cambridge, pp. 582–633.

Alonso, Y., 1998. Lateralization of visual guided behavior during feeding in zebra finches (*Taeniopygia guttata*). Behavioural Processes 43, 257–263.

Anokhin, K.V., Tiunova, A., 1996. Interocular transfer of learning associated with the formation of categoric memory in chicks. Proceedings of the Russian Academy of Sciences 348, 564–566.

Bennett, A.D.T., Cuthill, I.C., 1994. Ultraviolet vision in birds: what is the function? Vision Research 34, 1471–1478.

Blough, P.M., 1989. Attentional priming and visual search in pigeons. Journal of Experimental Psychology: Animal Behavior Processes 15 (4), 358–365.

Bond, A.B., 1983. Visual search and selection of natural stimuli in the pigeon: the attention threshold hypothesis. Journal of Experimental Psychology: Animal Behavior Processes 9 (3), 292–306.

Bond, A.B., Kamil, A.C., 1998. Apostatic selection by blue jays produces balanced polymorphism in virtual prey. Nature 395, 594–596.

Bond, A.B., Kamil, A.C., 1999. Searching image in blue jays: facilitation and interference in sequential priming. Animal Learning & Behavior 27 (4), 461–471.

Bond, A.B., Kamil, A.C., 2002. Visual predators select for crypticity and polymorphism in virtual prey. Nature 415, 609–613.

Bradshaw, J.L., Rogers, L.J., 1993. The Evolution of Lateral Asymmetries, Language, Tool Use, and Intellect. Academic Press Inc., San Diego.

Clayton, N., 1993. Lateralization and unilateral transfer of spatial memory in marsh tits. Journal of Comparative Physiology A 171, 799–806.

Cowan, W.M., Adamson, L., Powell, T.P.S., 1961. An experimental study of the avian visual system. Journal of Anatomy 95, 545–563.

Dawkins, M., 2002. What are birds looking at? Head movements and eye use in chickens. Animal Behaviour 63, 991–998.

Diekamp, B., Prior, H., Güntürkün, O., 1999. Lateralization of serial color reversal learning in pigeons (*Columba livia*). Animal Cognition 2, 187–196.

Dukas, R., Kamil, A.C., 2001. Limited attention: the constraint underlying search image. Behavioral Ecology 12 (2), 192–199.

Feare, C., 1984. The Starling. Oxford University Press, Oxford.

Gaston, K.E., 1984. Interocular transfer of pattern discrimination learning in chicks. Brain Research 310, 213–221.

Goodale, M.A., 1985. Interocular transfer in the pigeon after lesions of the dorsal supraoptic decussation. Behavioral Brain Research 16, 1–7.

Goodale, M.A., Graves, J.A., 1982. Interocular transfer in the pigeon: retinal locus as a factor. In: Ingle, D.J., Goodale, M.A., Mansfield, R.J.W. (Eds.), Analysis of Visual Behavior. MIT Press, Cambridge, pp. 211–240.

Guilford, T., Dawkins, M.S., 1987. Search images not proven: a reappraisal of recent evidence. Animal Behaviour 35, 1838–1845.

Güntürkün, O., 2002. Ontogeny of visual asymmetry in pigeons. In: Rogers, L.J., Andrew, R.J. (Eds.), Comparative Vertebrate Lateralization. Cambridge University Press, Cambridge, pp. 247–373.

Güntürkün, O., Hahmann, U., 1994. Visual acuity and hemispheric asymmetries in pigeons. Behavioral Brain Research 60, 171–175.

Güntürkün, O., Kischkel, K.-F., 1992. Is visual lateralization in pigeons sex-dependent? Behavioural Brain Research 47, 83–87.

Hart, N.S., Partridge, J.C., Cuthill, I.C., 2000. Retinal asymmetry in birds. Current Biology 10, 115–117.

Horn, G., 1991. Imprinting and recognition memory; a review of neural mechanisms. In: Andrew, R.J. (Ed.), Neural and Behavioral Plasticity: The Domestic Chick as a Model. Oxford University Press, Oxford, pp. 219–261.

Langley, C.M., 1996. Search images: selective attention to specific visual features of prey. Journal of Experimental Psychology: Animal Behavior Processes 22 (2), 152–163.

Martin, G.R., 1986. The eye of a passeriform bird, the European Starling, *Sturnus vulgaris*: eye movement amplitude, visual fields and schematic optics. Journal of Comparative Physiology 159, 545–547.

Mench, J.A., Andrew, R.J., 1986. Lateralization of a food search task in the domestic chick. Behavioral and Neural Biology 46, 107–114.

Nottelmann, F., Wohlschlager, A., Güntürkün, O., 2002. Unihemispheric memory in pigeons—knowledge, the left hemisphere is reluctant to share. Behavioural Brain Research 133, 309–315.

Pietrewicz, A.T., Kamil, A.C., 1979. Search image formation in the blue jay (*Cyanocitta cristata*). Science 204, 1332–1333.

Pietrewicz, A.T., Kamil, A.C., 1981. Search images and the detection of cryptic prey: an operant approach. In: Kamil, A.C., Sargent, T.D. (Eds.), Foraging Behavior: Ecological, Ethological, and Psychological Approaches. Garland, New York, pp. 311–331.

Plaisted, K.C., Mackintosh, N.J., 1995. Visual search for cryptic stimuli in pigeons: Implications for the search image and search rate hypotheses. Animal Behaviour 50, 1219–1232.

Reid, P.J., Shettleworth, S.J., 1992. Detection of cryptic prey: search image or search rate? Animal Behavior Processes 18 (3), 273–286.

Remy, M., Watanabe, S., 1993. Two eyes and one world: studies of interocular and intraocular transfer in birds. In: Ziegler, P., Bischoff, H. (Eds.), Vision, Brain & Behavior in Birds. MIT Press, Massachusetts, pp. 333–350.

Robinson, S.R., 1994. Early vertebrate color vision. Nature 367, 121.

Rogers, L.J., 1997. The Development of Brain and Behaviour in the Chicken. CABI Publishing, Oxford.

Rogers, L.J., 2002. Advantages and disadvantages of lateralization. In: Rogers, L.J., Andrew, R.J. (Eds.), Comparative Vertebrate Lateralization. Cambridge University Press, Cambridge, pp. 126–153.

Rose, S.P., 1991. How chicks make memories: the cellular cascade from c-fos to dendritic remodeling. Trends in Neurosciences 14, 390–397.

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.

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.

Skiba, M., Diekamp, B., Prior, H., Güntürkün, O., 2000. Lateralized interhemispheric transfer of color cues: evidence for dynamic coding principles of visual lateralization in pigeons. Brain and Language 73, 254–273.

Templeton, J.J., Gonzalez, D.P., 2004. Reverse lateralization of visual discriminative abilities in the European Starling. Animal Behaviour 67, 783–788.

Tinbergen, L., 1960. Control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. Archives Nerlandaises de Zoologie (Leiden) 13, 265–343.

von Fersen, L., Güntürkün, O., 1990. Visual memory lateralization in pigeons. Neuropsychologia 28 (1), 1–7.

Vorobyev, M., Osorio, D., Bennett, A.T.D., Marshall, N.J., Cuthill, I.C., 1998. Tetrachromacy, oil droplets and bird plumage colours. Journal of Comparative Physiology A 183, 621–633.

Vreven, D., Blough, P.M., 1998. Searching for one or many targets: effects of extended experience on the runs advantage. Journal of Experimental Psychology: Animal Behavior Processes 24 (1), 98–105.

Watanabe, S., Hodos, W., Bessette, B.B., 1984. Two eyes are better than one: superior binocular discrimination learning in pigeons. Physiology & Behavior 32, 847–850.

Weidner, C., Reperant, J., Miceli, D., Haby, M., Rio, J.P., 1985. An anatomical study of ipsilateral projections in the quail using radiographic, horseradish peroxidase, fluorescence and degenerative techniques. Brain Research 340, 99–108.

Wilkinson, L., 1990. SYSTAT: The System for Statistics. SYSTAT, Inc., Evanston, IL.