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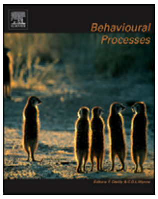

A behavioral analysis of prey detection lateralization and unilateral transfer in European starlings (*Sturnus vulgaris*)

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ABSTRACT

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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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.

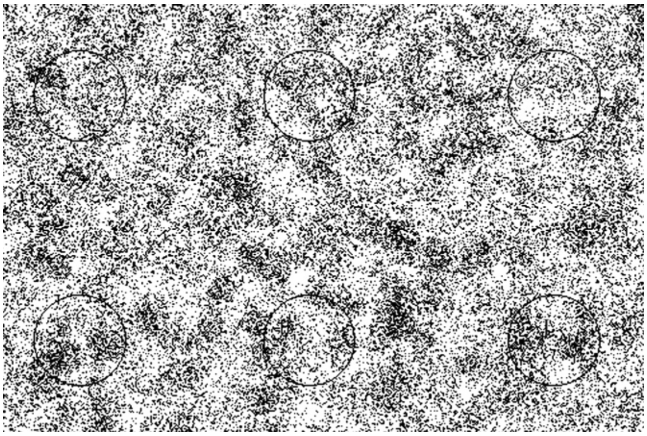

Fig. 1. Section of experimental background showing the six cues in the top left quadrant of each circle. From left to right: triangle Δ; delta ∂; happy face ☺; female symbol ♀, H, and J. Cues were not always in the same locations within the circles. Circles indicated the location of wells.

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.