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An eye for beauty: Lateralized visual stimulation of courtship behavior and mate preferences in male zebra finches, *Taeniopygia guttata*

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ABSTRACT

Research on intersexual selection focuses on traits that have evolved for attracting mates and the consequences of mate choice. However, little is known about the cognitive and neural mechanisms that allow choosers to discriminate among potential mates and express an attraction to specific traits. Preferential use of the right eye during lateral displays in zebra finches, and lateralized expression of intermediate early genes in the left hemisphere during courtship led us to hypothesize that: (1) visual information from each eye differentially mediates courtship responses to potential mates; and (2) the ability to discriminate among mates and prefer certain mates over others is lateralized in the right eye/left hemisphere system of zebra finch brains. First, we exposed male zebra finches to females when using left, right or both eyes. Males courted more when the right eye was available than when only the left eye was used. Secondly, male preference for females – using beak color to indicate female quality – was tested. Right-eyed and binocular males associated with and courted orange-beaked more than gray-beaked females; whereas left-eyed males showed no preference. Lateral displays and eye use in male zebra finches increase their attractiveness and ability to assess female quality, potentially enhancing reproductive success.

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1. Introduction

Research on intersexual selection has focused intensively on traits that have evolved for attracting mates and the consequences of mate choice (Andersson, 1994). However, little is known about the cognitive and neural mechanisms that allow the chooser to discriminate visually between different potential mates and to express an attraction to certain traits (Fisher et al., 2002, 2005; Ryan et al., 2009; Sockman, 2007; Wong et al., 2012). Reports that immediate early gene (IEG) expression in the avian brain is associated with sexual behavior have provided some preliminary evidence for the neural basis of such mechanisms (reviewed by Ball and Balthazart, 2001).

IEGs are expressed when neurons fire; therefore, this is an indirect marker of neuronal activity. The IEGs zenk and *c-fos* are expressed in high concentrations in the brain during sexual imprinting, early courtship, and song production in the domesticated zebra finch (*Taeniopygia guttata*), an estrildid finch native to Australia. Most interestingly, the IEG response is asymmetrically higher in various regions of the left hemisphere during all of these activities (Avey et al., 2005; George et al., 2006; Lieshoff et al., 2004); for example, densities of ZENK-immunoreactive neurons are significantly higher in the left optic tectum than the right following courtship (George et al., 2006). These findings led us to hypothesize: (1) that visual stimulation of courtship behavior and singing may be lateralized in the right eye/left hemisphere system; and (2) that the ability to discriminate visually among mates and to prefer certain mates over others may also be lateralized in the right eye/left hemisphere system of the zebra finch brain.

Functional lateralization refers to the specialization of each brain hemisphere for different cognitive, perceptual and behavioral tasks (Rogers and Andrew, 2002; Rogers et al., 2013; Vallortigara and Rogers, 2005). Hemispheric specialization theoretically has adaptive value because it eliminates neural redundancy while increasing performance efficiency (Rogers and Andrew, 2002). It also enables individuals to perform important tasks, like foraging and vigilance or sleeping and vigilance, simultaneously (Franklin and Lima, 2001; Rattenborg et al., 1999; Rogers et al., 2004). Vallortigara and Rogers (2005, p. 581) have proposed that certain cognitive skills might be more likely to show "directional asymmetry" (i.e. consistent lateralization at the population level) due to "the need to coordinate behavior among behaviorally asymmetric individuals". Courtship fits this type of behavior pattern and several taxonomic groups show consistent lateralized responses in the context of courtship and copulation-solicitation behaviors, including

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lizards (Hews et al., 2004), fish (Dadda and Bisazza, 2006), and birds (George et al., 2006; Rogers et al., 1985; Workman and Andrew, 1986). Lateral courtship displays in which the male presents one flank to the female or uses one eye to view the female are also widespread in various avian species under natural and captive conditions (Andrew, 1961; Rosa Salva et al., 2012; Ventolini et al., 2005; Workman and Andrew, 1986). For example, Workman and Andrew (1986, 1991) reported that captive, domesticated male zebra finches preferentially used their right eye when approaching and viewing a female during the silent, static phase of courtship, a behavioral asymmetry at the population level that is consistent with the lateralized expression of IEGs in the zebra finch brain described above. ten Cate et al. (1990) and ten Cate (1991) argued against Workman and Andrew's interpretation, stating that male orientation could have been influenced either by female orientation (because they were together in the same cage) or by a locomotor bias in which birds preferentially move in a particular direction past potential mates, thus apparently using a particular eye simply due to the direction of movement. When ten Cate et al. (1990) tested these hypotheses in a very different experimental set up from Workman and Andrew (1986), a locomotor bias was indeed found in females but this bias did not appear to contribute to a corresponding asymmetry in eye use (ten Cate et al., 1990; ten Cate, 1991). Despite these differences in interpretation, both Workman and Andrew (1991) and ten Cate (1991) agreed that research on lateralization of courtship behavior should continue.

Birds lack a corpus callosum, the bundle of neural fibers found in the brains of placental mammals that transmits information between the two hemispheres; in addition, the optic nerve from each eye in birds transmits almost all visual information to the contralateral hemisphere (Cowan et al., 1961). Although 'interocular transfer' of information between the hemispheres is possible via the supraoptic decussation, this can be delayed by several hours (e.g. Clayton, 1993). Thus, researchers have found that the simple, non-invasive technique of monocular occlusion – literally, 'one eye covered' – allows one to test for a variety of visual and hemispheric specializations in birds, including spatial memory (Clayton, 1993; Sherry et al., 1981), visual discrimination (Güntürkün, 1997; Templeton and Gonzalez, 2004), and prey detection (Alonso, 1998; Templeton and Christensen-Dykema, 2008).

Here, we present two experiments in which we examine lateralized visual stimulation of courtship behavior and visual lateralization of mate choice in male zebra finches. We chose to test males because female zebra finches tend to base their mate preferences on male song, rather than on male appearance (e.g. Collins et al., 1994; but see Simons and Verhulst, 2011). In the first experiment, we considered the hypothesis that visual sexual information – specifically, the opportunity to view females – stimulates courtship behavior differently depending on which hemisphere processes this information. We tested this hypothesis by measuring two aspects of courtship behavior under binocular and monocular conditions: attention to females and directed song. If the courtship sequence is initiated in the right eye/left hemisphere system of the brain, the males should pay more attention and sing more to females when the right eye is available than when only the left eye is used.

The second experiment investigated whether the ability to express a visual preference for a particular female type is also lateralized in the right eye/left hemisphere system of the male zebra finch brain. Using short-term, two-choice trials (Rutstein et al., 2007; Murphy et al., 2009), male sexual preference for particular females – based on beak color as an indicator of female quality (Burley and Coopersmith, 1987; Simons et al., 2012) – was tested under monocular and binocular conditions. We predicted that right-eyed and binocular males should preferentially associate with and sing to orange-beaked ("mature") females as opposed to gray-beaked ("immature") females. In contrast, left-eyed males were predicted to show an equal preference for both female types.

2. Experiment 1

2.1. Methods

2.1.1. Subjects and apparatus

Twenty-four adult male and three adult female (wild type, piebald, white morph) domesticated zebra finches were obtained from a local pet store three months prior to this experiment. All subjects previously had been tested in an unrelated behavioral experiment. Birds were housed in single-sex holding cages (44 cm × 44 cm × 55 cm) with two to three birds per cage until the night before trials were conducted. The males had been isolated from the females in a different holding room for at least three months prior to testing. The parentage of the males – and thus their preferred female type – was unknown, thus each male was tested in the presence of all three females. The finches were maintained on a 14:10 light–dark cycle with full spectrum lighting at 22 °C, and were given Wild Harvest® Daily Blend for Parakeet, Canary and Finch, with water ad libitum, except during experimental trials.

The male test cage was a holding cage, but it had one side replaced with transparent acrylic and contained two perches 30 cm from the cage floor and approximately 5 and 25 cm from the acrylic. The male was stimulated to court by the presence of three female finches held in an adjacent cage. The female cage also had a clear acrylic wall, with only one perch 5 cm from the acrylic to keep the stimulus females close to the male. The two cages were positioned with the acrylic sides touching each other during trials. There were three eye conditions: binocular – both eyes available and eye rings around each eye; right monocular – left eye occluded, and left monocular – right eye occluded. Eye rings, teardrop-shaped loops of hemp twine (8 mm diam.), were attached with Ardell® eyelash adhesive around both eyes of each male subject 24 h prior to the first trial and were worn for the three days of testing. Under monocular conditions, a temporary eye cap, a small cone made of opaque cotton cloth, was glued to the appropriate eye ring, occluding one eye and impeding direct visual stimulation of the contralateral hemisphere. The cap was removed after each trial. This eye ring and cap method of monocular occlusion causes finches little discomfort (Templeton et al., 2012). Birds in this and the following experiment either were returned to the pet store where they were purchased or were retained for future experiments.

2.1.2. Procedure

Subjects were tested once under each of the three eye conditions over three consecutive days; order of testing was balanced over all subjects. A subject male was moved to a testing cage within the same holding room 24 h prior to testing. Three subject males were tested individually per day. There was a 30-min acclimation period before each trial to allow the bird to recover from handling during eye cap placement, whether an eye cap was used or not. During the acclimation period, an opaque barrier was set between the acrylic sides of the solitary male and the stimulus female cages. Removing the barrier signaled the beginning of each trial. Trials were 10 min in duration. The same stimulus females were used in all trials. The procedures used in this and the following experiment were approved by the Institutional Animal Care and Use Committee of Knox College, and adhered to the *Guidelines for the Use of Animals in Research*.

2.1.3. Data collection and analyses

All 72 trials were recorded using a Digital Sony Camcorder (Model: DCR-TRV280). Behavioral data collected while scoring

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