In the eye of the beholder: visual mate choice lateralization in a polymorphic songbird

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Birds choose mates on the basis of colour, song and body size, but little is known about the mechanisms underlying these mating decisions. Reports that zebra finches prefer to view mates with the right eye during courtship, and that immediate early gene expression associated with courtship behaviour is lateralized in their left hemisphere suggest that visual mate choice itself may be lateralized. To test this hypothesis, we used the Gouldian finch, a polymorphic species in which individuals exhibit strong, adaptive visual preferences for mates of their own head colour. Black males were tested in a mate-choice apparatus under three eye conditions: left-monocular, right-monocular and binocular. Three stimulus birds were available for viewing in each trial: a black male, red females or black males when their right eye was available. Beauty, therefore, is in the right eye of the beholder for these songbirds, providing, to our knowledge, the first demonstration of visual mate choice lateralization.

Keywords: visual lateralization; mate choice; polymorphic; finch

1. INTRODUCTION

Making an appropriate mate choice is one of the most important and complex decisions an individual faces in life. Many bird species base their mate preferences on conspicuous visual and auditory traits such as colour, song and body size, and research on intersexual selection has focused intensively on traits that have evolved owing to mate attraction and the consequences of mate choice [1]. However, until recently, surprisingly little attention has been paid to the mechanisms that allow the chooser to discriminate visually among different potential mates and to express a preference for certain traits [2–4].

Lateral courtship displays are well known in birds [5], and some species also show preferential use of a particular eye during courtship [6]. For example, zebra finch (Taeniopygia guttata) males apparently prefer to view females with the right eye during the static phase of courtship [7]. This population-level asymmetry in zebra finch courtship behaviour corresponds with recent reports of asymmetries in immediate early gene (IEG) expression in the songbird brain in response to sexual stimuli. Expression of IEGs is an indirect marker of neuronal activity, because IEGs are expressed when neurons fire. Interestingly, IEG expression is consistently higher in the left hemisphere than the right during sexual imprinting, early courtship and song production in zebra finches [8–10]. These functional asymmetries in the processing of visual courtship signals in zebra finches led us to hypothesize that the ability to discriminate visually among mates and to express a preference for certain mates may be lateralized in the right-eye/left-hemisphere system of the songbird brain.

Functional lateralization is the specialization of each hemisphere for different cognitive, perceptual and behavioural tasks [6,11]. In birds, the optic nerve from each eye transmits visual information to the contralateral hemisphere; in addition, birds lack the corpus callosum that allows communication between the hemispheres in placental mammals. Although the supraoptic decussation enables interhemispheric information transfer in birds, this takes several hours [12]. Thus, the simple, non-invasive technique of monocular occlusion [11] allows us to test for hemispheric specialization of mate choice in birds.

Testing the hypothesis that visual mate preferences are lateralized in the right-eye/left-hemisphere system requires a species that has strong preferences for specific visual characteristics in the opposite sex. We chose the Gouldian finch (Erythrura gouldiae), an estrildid finch native to northern Australia that has a genetically based colour polymorphism with three head colours: black, red and the rare yellow morph (<1% adults). Both black and red morphs strongly prefer mates of their own morph [13], which is adaptive because of genetic incompatibilities between interbreeding morphs [14].

We tested short-term mating preferences of black males under three eye conditions: left-monocular, right-monocular and binocular. Three stimulus birds were available for viewing in each trial: a black male, and two females—one red, one black. Black males were predicted to show a greater preference for black females when using their right eye or both eyes than when using the left eye alone. We also predicted that black males would prefer black females more than red females or black males when their right eye was available, but not when only the left eye was available.

2. MATERIAL AND METHODS

(a) Subjects and apparatus

Owing to logistical constraints, only black males, which show the strongest preferences for mates of the same morph [15], were used. Sixteen homozygous black males from the Save the Gouldian Fund facility [15] were tested during the breeding season. All birds were sexually naive adults held in single sex/head-colour cages (75 × 40 × 30 cm) in auditory, but not visual contact with members of the opposite sex. Each subject also served as a stimulus bird; thus, there were 16 black stimulus males, plus 16 red and 12 black stimulus females.
To black females was significantly stronger ($F_{1,121} = 33$, $p = 0.003$; figure 1a). Contrast analyses showed that black males spent significantly less time viewing black females when using their left eye than they did when using their right eye or both eyes ($F_{1,121} = 9.3$, $p < 0.003$; figure 1a).

Controlling for eye treatment, black male response to black females was significantly stronger ($F_{1,121} = 3.8$, $p = 0.029$) than they did when using their right eye or both eyes ($F_{1,121} = 1.7$, $p = 0.12$). There were significant effects of both eye and stimulus on proportion of time black males spent (a) closely viewing or (b) singing to stimuli from adjacent choice zones (arcsine-transformed data). (JMP calculates a fractional denominator degree of freedom (d.f.) to account for an unbalanced design with a random factor. See LS means tables in the electronic supplementary material, appendix.)
Courtship and reproductive fighting: a review. Ibis 103, 315–348.

4. DISCUSSION

Eye availability plays a crucial role in black male Gouldian finches’ preferences for associating with and courting different social stimuli. Black females were strongly preferred over red females and black males, but only in the right-eyed and binocular conditions; left-eyed males were unable to respond discriminatively, not only to black males and females, but also to the two very different female morphs. Eye availability also affected courtship song production; more males sang to black females, but only when the right eye was available. These results offer compelling evidence that the ability to express a preference for a particular morph is constrained to the right-eye/left-hemisphere system, thus providing, to our knowledge, the first demonstration of visual mate choice lateralization in any animal.

These findings are consistent with the recent proposal that the left hemisphere in many taxa is specialized to distinguish between conspecifics and heterospecifics [6]—or between two different morphs in the case of Gouldian finches. Our results may also help to explain why so many courtship rituals in birds include lateral displays [5,6]. This type of courtship behaviour has sometimes been explained as males ‘showing their best side’ [17] but viewing females with a particular eye during courtship can also stimulate an enhanced courtship display [10]. Most importantly, in Gouldian finches, for whom choosing the wrong mate can have dire fitness consequences [14], preferential eye use should also facilitate adaptive mate choice—saving courtship time and energy [2], and ultimately increasing reproductive success.

Our results add mate choice, a process of great adaptive significance, to the extensive list of cognitive and behavioural functions known to be lateralized [11]. Understanding the mechanisms underlying mate choice and identifying the specific brain regions involved may lead to new insights into sexual selection and speciation [2–4].

All procedures approved by Macquarie University’s Institutional Animal Care and Ethics Committee.

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