

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. We found that black male preference for black females is so strongly lateralized in the right-eye/left-hemisphere system that if the right eye is unavailable, males are unable to respond preferentially, not only to males and females of the same morph, but also to the strikingly dissimilar female morphs. Courtship singing is consistent with these lateralized mate preferences; more black males sing to black females when using their right eye than when using their left. 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].

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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.

Table 1. Results of GLMM analysis, testing effects of 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.)

effect	<i>F</i>	d.f.	<i>p</i>
(a) eye (left, right, both)	3.4	2, 121	0.04
stimulus (black female, red female, black male, empty chamber)	6.2	3, 121	0.0006
stimulus × eye	1.7	6, 121	0.12
(b) eye (left, right, both)	2.0	2, 48.34	0.148
stimulus (black female, red female)	1.4	1, 48.34	0.247
stimulus × eye	3.8	2, 46.13	0.029

Unique combinations of three unfamiliar stimulus birds, one black male and two females—one red, one black—were used for each subject's trial. The fourth stimulus chamber (see below) remained empty. Rings of string (1 mm thick, 8 mm diameter) were attached with non-toxic, waterproof, Ardell eyelash glue to the feathers around both eyes of each bird. For monocular occlusion trials, a cone of opaque, white cotton was attached to a ring 15 min prior to the start of a test trial, and removed afterwards. The finches readily accepted these eye caps, which effectively occlude vision [16].

The mate-choice apparatus [15] had a central arena (33 × 33 × 15 cm), plus four stimulus chambers (15 × 33 × 15 cm), separated from adjacent choice zones (12 × 33 × 15 cm) by clear acrylic glass. Perches were available on either side of each partition. Trials were videotaped from above using a Sony digital camcorder (model DCR-HC96).

(b) Procedure

Subjects were tested once per day over three consecutive days, each time with a different eye and a different set of three stimulus birds and chamber locations. Eye condition order was balanced over individuals. Fifteen minutes prior to the start of a test trial, a subject was placed in the central arena to acclimate. Stimulus birds were put in their chambers at the start of the 45 min trial. Actual trial duration depended on the time at which a subject began to move (mean duration ± s.d. = 44 : 19 ± 5 : 31). Thus, trial durations were not the same for all birds. Only subjects that began moving around the arena within 30 min on all three trials (12 males) were included in analyses.

Mate choice in birds is typically measured by proximity to and courtship of the preferred type. Data analysed included the proportion of total trial time spent viewing each of the stimulus chambers from the adjacent choice zone (trial time included time spent in the central arena), and the proportion of total courtship singing directed to each of the stimulus females. All proportions were arcsine-transformed to normalize the data for analysis. Trials were scored blindly; stimulus birds were not visible to the observer. A naive individual rescored 12 of 36 trials, randomly selected with the constraint that there were four trials of each eye condition; inter-observer reliability (correlation coefficient) was 0.90 for proportion of time spent viewing each stimulus.

We analysed preference and song data on JMP v. 9.0.3 with a generalized linear mixed model (GLMM) using REML estimation, with male identity as a random factor to account for repeated measures. We then performed planned contrast analyses: (i) to compare the responses of black males using their left eye to those using their right or both eyes when viewing black females, and (ii) to compare the responses of males to black and red females and black males, controlling for eye treatment.

3. RESULTS

There were significant effects of both eye and stimulus on the proportion of time that black males spent closely viewing the stimulus birds (table 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 ($F_{1,121} =$

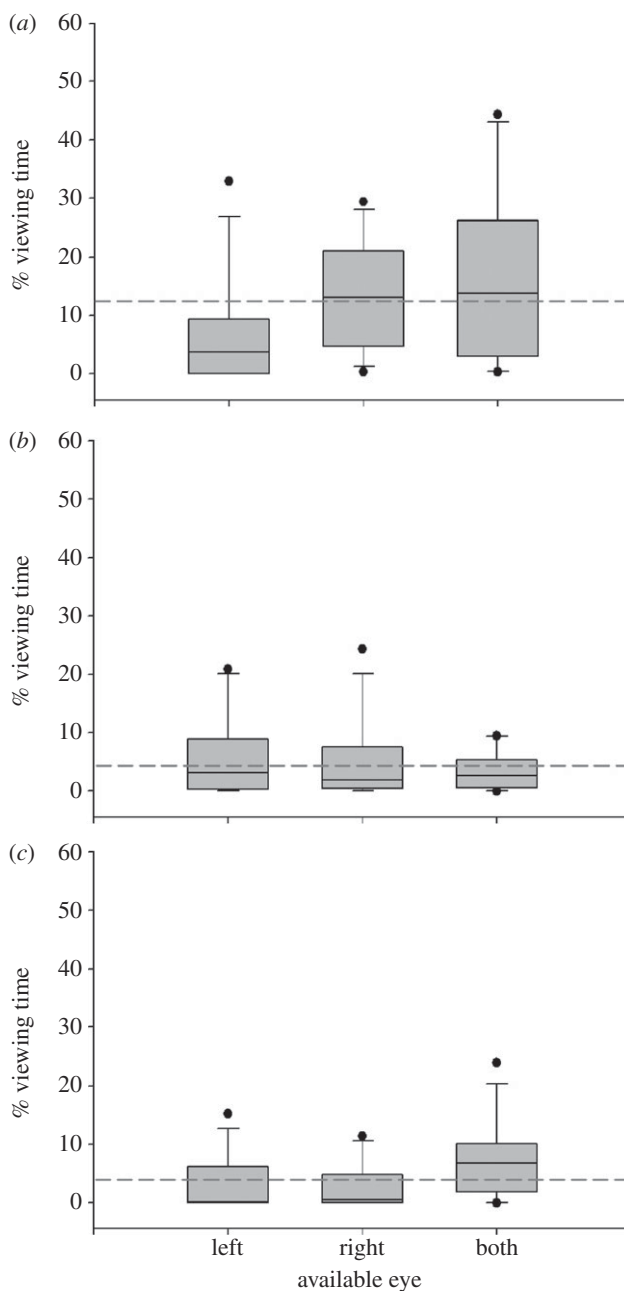


Figure 1. (a–c) Box plots of the per cent total trial time that black males ($n = 12$) in each eye condition closely viewed social stimuli from adjacent choice zones. Horizontal dashed line denotes overall mean. (a) Black female, (b) red female and (c) black male.

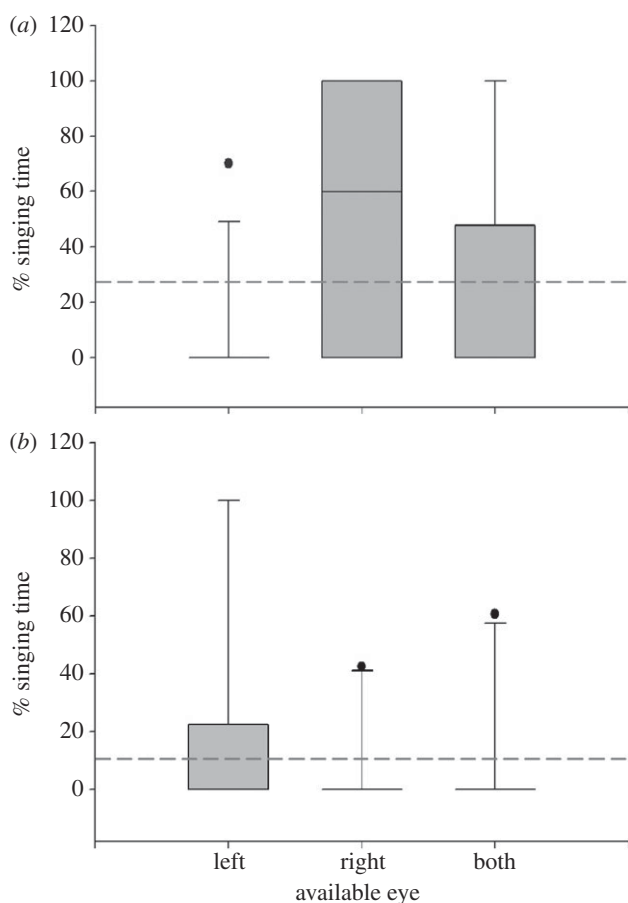


Figure 2. (a,b) Box plots of the per cent total singing time that black males ($n = 12$) in each eye condition sang to both female morphs. Horizontal dashed line denotes overall mean. (a) Black female, (b) red female.

17.9, $p < 0.0001$) than to red females and black males (figure 1a–c). Right-eyed males spent a significantly greater proportion of trial time closely viewing black females than red females, black males or the empty chamber ($F_{1,33} = 7.71$, $p = 0.009$), as did males using both eyes ($F_{1,33} = 7.32$, $p = 0.012$). Conversely, left-eyed males showed no significant differences in their preferences for the four stimuli ($F_{1,33} = 0.281$, $p = 0.600$).

Eight of 12 males sang to at least one female on at least one of their three trials; subjects never sang to males. There was a significant interaction between available eye and female colour (table 1b), implying that males were more likely to sing to red females when using their left eye and to black females when using their right eye (figure 2a,b). Contrast analysis comparing the proportion of time males spent singing to black females when using their left eye versus the right or both eyes was not significant ($F_{1,46.7} = 2.9$, $p = 0.093$). However, more males sang for a greater proportion of time to black females when using their right eye than when using their left (7 versus 0, sign test: $p < 0.05$); only one male sang to a black female when using its left eye.

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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- Andersson, M. 1994 *Sexual selection*. Princeton, NJ: Princeton University Press.
- Fisher, H., Aron, A., Mashek, D., Strong, G., Li, H. & Brown, L. 2002 Neural mechanisms of mate choice: a hypothesis. *Neuroendocrinol. Lett.* **23**(Suppl. 4), 92–97.
- Pelphs, S. M., Rand, A. S. & Ryan, M. J. 2006 A cognitive framework for mate choice and species recognition. *Am. Nat.* **167**, 28–42. (doi:10.1086/498538)
- Ryan, M. J., Akre, K. L. & Kirkpatrick, M. 2009 Cognitive mate choice. In *Cognitive ecology II* (eds R. Dukas & J. Ratcliffe), pp. 137–155. Chicago, IL: University of Chicago Press.
- Andrew, R. J. 1961 The displays given by passerines in courtship and reproductive fighting: a review. *Ibis* **103**, 315–348.
- Salva, O. R., Regolin, L., Mascalcioni, E. & Vallortigara, G. 2012 Cerebral and behavioural asymmetries in

- animal social recognition. *Comp. Cogn. Behav. Rev.* **7**, 110–138. (doi:10.3819/ccbr.2012.70006)
- 7 Workman, L. & Andrew, R. J. 1986 Asymmetries of eye use in birds. *Anim. Behav.* **34**, 1582–1584. (doi:10.1016/S0003-3472(86)80235-4)
- 8 Lieshoff, C., Grosse-Ophoff, J. & Bischoff, H. 2004 Sexual imprinting leads to lateralized and non-lateralized expression of the immediate early gene *zenk* in the zebra finch brain. *Behav. Brain Res.* **148**, 145–155. (doi:10.1016/S0166-4328(03)00189-X)
- 9 Avey, M., Philmore, L. & MacDougall-Shackleton, S. 2005 Immediate early gene expression following exposure to acoustic and visual components of courtship in zebra finches. *Behav. Brain Res.* **165**, 247–253. (doi:10.1016/j.bbr.2005.07.002)
- 10 George, I., Hara, E. & Hessler, N. 2006 Behavioral and neural lateralization of vision in courtship singing of the zebra finch. *J. Neurobiol.* **66**, 1164–1173. (doi:10.1002/neu.20273)
- 11 Vallortigara, G. & Rogers, L. 2005 Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. *Behav. Brain Sci.* **28**, 575–633. (doi:10.1017/S0140525X05000105)
- 12 Clayton, N. 1993 Lateralization and unilateral transfer of spatial memory in marsh tits. *J. Comp. Physiol. A* **171**, 799–806. (doi:10.1007/BF00213076)
- 13 Pryke, S. R. 2010 Sex chromosome linkage of mate preferences and colour signal maintains assortative mating between interbreeding finch morphs. *Evolution* **64**, 1301–1310. (doi:10.1111/j.1558-5646.2009.00897.x)
- 14 Pryke, S. R. & Griffith, S. C. 2009 Postzygotic genetic incompatibility between sympatric colour morphs. *Evolution* **63**, 793–798. (doi:10.1111/j.1558-5646.2008.00584.x)
- 15 Pryke, S. R. & Griffith, S. C. 2007 The relative role of male versus female mate choice in maintaining assortative pairing among discrete colour morphs. *J. Evol. Biol.* **20**, 1512–1521. (doi:10.1111/j.1420-9101.2007.01332.x)
- 16 Templeton, J. J. & Gonzalez, D. P. 2004 Reverse lateralization of visual discriminative abilities in the European starling. *Anim. Behav.* **67**, 783–788. (doi:10.1016/j.anbehav.2003.04.011)
- 17 Gross, M. R., Suk, H. Y. & Robertson, C. T. 2007 Courtship and genetic quality: asymmetric males show their best side. *Proc. R. Soc. B* **274**, 2115–2122. (doi:10.1098/rspb.2007.0432)