



Research report

Hemispheric specialization in Australian magpies (*Gymnorhina tibicen*) shown as eye preferences during response to a predator

Adam Koboroff*, Gisela Kaplan¹, Lesley J. Rogers²

Centre for Neuroscience and Animal Behaviour, School of Science and Technology, University of New England, Armidale, NSW 2351, Australia

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ABSTRACT

Brain lateralization in birds is frequently expressed as a preference to view stimuli with one eye using the lateral monocular visual field. As few studies have investigated lateralized behaviour in wild birds, we scored eye preferences of Australian magpies (*Gymnorhina tibicen*) performing anti-predator responses. When animals deal with potential predators by mobbing them, constant assessment is needed to consider whether to approach, mob or withdraw. When presented with a taxidermic specimen of a monitor lizard, the magpies assembled on the ground close to the lizard and circled, pecked, jumped over, viewed and approached, or withdrew from it. Using video footage, the monocular fixations prior to or during performance of these activities were scored and the following significant eye preferences were found. Prior to withdrawing, the magpies viewed the lizard with the left eye (LE) (85% of events). Prior to approaching, the right eye (RE) was used (72%). Hence, the left hemisphere is used to process visual inputs prior to approaching the predator and the right hemisphere prior to withdrawing from it. This result is consistent with hemispheric specialization shown in other species, including humans. The LE was used also prior to jumping (73%) and prior to circling (65%), as well as during circling (58%) and for high alert inspection of the predator (72%). Mobbing and perhaps circling are agonistic responses controlled by the LE/right hemisphere, as also seen in other species. Alert inspection involves detailed examination of the predator and likely high levels of fear, known to be right hemisphere function.

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1. Introduction

Lateralization of the brain, which refers to the ability of the two hemispheres of the brain to conduct different functions, is common in vertebrates and particularly strong in birds at both the structural and functional levels of organization [24]. In birds that have their eyes positioned on the sides of the head, laterality can be determined by scoring left and right eye use to view a particular object/stimulus [17,21].

Lateralization in birds has been studied primarily using tests conducted in the laboratory, mainly on domestic chicks [23] and pigeons [10]. In fact, very few studies have investigated lateralized visual processing in wild birds. Franklin and Lima [9] tested wild juncos as they fed alongside a wall and the juncos preferred to position themselves so that they could monitor the surrounds with one eye. Research into laterality of blacked-winged stilts (*Himantopus himantopus*) found a population bias for capture of prey on the right side and courtship behaviour on the left side [32]. Rogers

[19] reported a left eye (LE) preference in kookaburras (*Dacelo novaeguineae*) to view the ground in search of moving prey. Lastly, the Australian magpie (*Gymnorhina tibicen*) has been shown to exhibit preferred use of the LE prior to flying away from a human approaching the bird from behind [11].

Only two of the studies conducted on wild birds investigated vigilance [11,32], whereas vigilance or predator detection has received much attention in laboratory studies on laterality [14,22,26]. No previous study has investigated whether responses following detection of a predator (i.e. mobbing and other anti-predator behaviour) are lateralized.

We considered that it was likely that birds would show eye preferences as they approached a predator, either to inspect it or to mob it since approach to a predator requires continual assessment and decisions about whether to continue to approach or to withdraw (as studied in some detail in fish [8]). Avoidance and approach behaviour are likely to be controlled by different hemispheres of the brain and, based on previous research, it is likely that the left hemisphere (LH) controls approach and the right hemisphere (RH) withdrawal [2,5]. Alternatively, since mobbing may involve physical contact with a predator [27], it can be considered a strong agonistic response and such intense emotional responses are controlled by the RH, as shown in other vertebrates [6,18,31], including domestic chicks [30].

* Corresponding author. Tel.: +61 267 732 733; fax: +61 267 733 452.

E-mail addresses: akoborof@une.edu.au (A. Koboroff), gkaplan@une.edu.au (G. Kaplan), lrogers@une.edu.au (L.J. Rogers).

¹ Tel.: +61 267 753 113.

² Tel.: +61 267 723 969.

We chose the Australian magpie as an ideal species to investigate the possibility of eye preferences in reaction to a predator since mobbing of predators is common in their behavioural repertoire [13].

2. Materials and methods

Fifteen groups of wild magpies (2.68 ± 0.35 (mean \pm S.E.M.) birds per group) were selected on the basis of permanent occupation of a breeding territory. All groups were located in Armidale, NSW, Australia ($30^{\circ}32'S$, $151^{\circ}40'E$). Data were collected from December 2005 to June 2006. The experiments were conducted in the morning between 07:30 h and 10:00 h. The magpies were presented with a taxidermic model of a lace monitor lizard (*Varanus varius*). Each group was tested once or twice only and, for the groups that were presented with the lizard twice, pseudoreplication was avoided by identifying individual magpies and scoring a particular individual on only one of those tests. Individual magpies were identified by noting the wing markings [13], which can be used as a reliable identification marker. Data were collected for a total of 55 magpies.

The lizard was placed within the centre of the group's territory. This was done because several research papers [1,12,16] have reported that different levels of vigilance occur in the centre versus the periphery of the territory.

The experimenter stood behind a nearby feature (i.e. a building or tree) at least 20 m from the stimulus. Detection of the stimulus was noted when either alarm calls were emitted or at least one magpie approached within a 5 m radius of the stimulus. Following detection of the stimulus, video recordings commenced and continued for 5 min. The magpies usually detected the stimulus within five minutes of it being placed in the centre of their territory but a maximum time of 30 min was allowed for detection to occur.

During the presentations of the stimulus, the magpies assembled on the ground nearby the lizard and their behaviour was scored if they were within a 5 m radius of it. Eye preference was scored prior to the magpies withdrawing, approaching, jumping, pecking at the stimulus, circling or viewing it in an alert posture. Withdrawing and approaching were scored as walking or running (flying or jumping was not included) directly towards or away from the lizard, respectively. Jumping was scored as a brief vertical movement upwards, with both legs simultaneously off the ground, performed nearby the lizard or over it. Circling was scored as running or walking around the stimulus.

Eye use to fixate the stimulus prior to performing a particular behaviour was scored by replaying the videotape in slow-motion. A monocular fixation was scored when a magpie fixated the stimulus for at least one second at an angle of approximately 90° from the eye to the lizard (determined relative to the direction of the beak). Since the monocular visual fields of a magpie (laterally placed eyes) are $143\text{--}149^{\circ}$ on each side of the head and binocular field is $28\text{--}34^{\circ}$ frontal [25], the 90° angle was chosen to ensure that the fixation scored was indeed monocular.

Alert viewing was recorded only when magpies were (a) stationary, (b) had adopted a vigilance posture (neck extended, indicating high arousal, and feathers sleeked) and (c) were fixating the stimulus. Viewing was scored at the first fixation in a bout in which the magpie may have turned the head from side to side while standing stationary and alert. By recording only the first eye fixation on the stimulus during a viewing bout, runs were avoided.

Eye preferences during alert viewing were analysed in two categories, based on the overall response of the magpies during a presentation of the lizard: (A) tests in which mobbing occurred ($N=11$) and (B) tests in which only inspection and no mobbing occurred ($N=6$). During mobbing, most, if not all, of the members of the resident magpie group were recruited and the magpies vocalised continuously (86.2 ± 9.9 S.E.M. vocalisations per magpie per 5 min trial). Furthermore, during mobbing, the magpies also pecked at and jumped over the stimulus. By contrast, during inspection-only tests (B) only one magpie approached the lizard and no vocalisations, pecks or jumps were observed.

All scoring was conducted by AK, who was blind to the findings in this field. Inter-reliability tests were conducted with a naïve observer on the same behaviours and tapes used in this study and there was a strong and significant relationship between the two observers ($r=0.98$; $p=0.000$).

The data were analysed using a G -test (log-likelihood χ^2 -test), which analyses each individual's score whilst taking into account the number of scores per individual [28].

3. Results

The eye preferences are presented in Fig. 1. The percentages of LE preference were calculated as $LE/LE+RE \times 100$. There was a significant LE bias ($85.0\% \pm 4.2$ (mean \pm S.E.M.) LE) to view the lizard prior to the magpies withdrawing from it ($G_{(14)}=117.61$, $p<0.001$). By contrast, there was a significant RE bias ($27.6\% \pm 6.6$ (mean \pm S.E.M.) LE) to view the lizard prior to approaching it ($G_{(12)}=107.79$, $p<0.001$).

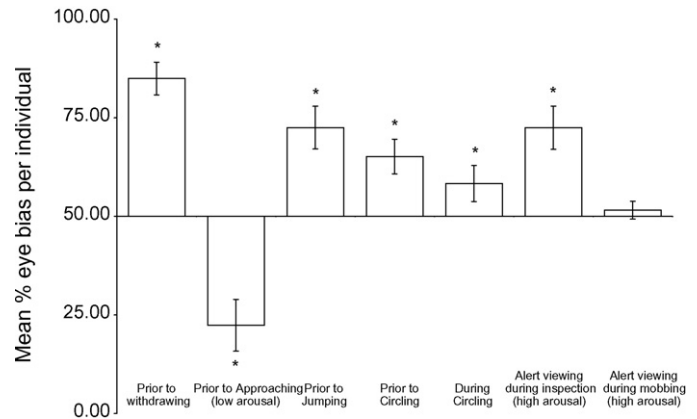


Fig. 1. Percentage eye bias is plotted as mean percent left eye preference for each of the behaviours scored, with standard errors. Values above 50% indicate a left eye and those below 50% a right eye bias. 50% indicates no bias. Asterisks indicate $p<0.001$.

Prior to jumping, the magpies viewed the lizard significantly more often with the LE ($72.5\% \pm 5.4$ (mean \pm S.E.M.) LE) than with the RE ($G_{(16)}=107.89$, $p<0.001$). Pecking was scored but there were insufficient data to analyse using a G -test. However, there was a suggestion that eye use prior to pecking was primarily with the LE ($82.0\% \pm 7.2$ (mean \pm S.E.M.), $N=6$).

Prior to circling the lizard, the magpies viewed the stimulus with a significant LE preference ($65.2\% \pm 4.4$ (mean \pm S.E.M.), $G_{(34)}=215.43$, $p<0.001$). During circling events, the significant LE bias continued as the direction of circling was predominately anti-clockwise ($58.3\% \pm 4.6$ (mean \pm S.E.M.), $G_{(23)}=111.47$, $p<0.001$).

There was a significant LE bias to adopt the alert posture and to view the lizard during inspection-only tests ($72.5\% \pm 5.5$ (mean \pm S.E.M.), $G_{(4)}=60.40$, $p<0.001$), but no significant eye bias to view the lizard in the alert posture during mobbing tests ($51.6\% \pm 2.2$ (mean \pm S.E.M.), $G_{(9)}=7.82$, $p>0.050$).

4. Discussion

Magpies show significant and often strong eye preferences prior to performing some types of anti-predator behaviour. They used the left eye/right hemisphere (LE/RH) prior to withdrawal and the right eye/left hemisphere (RE/LH) prior to an approach. The former result is consistent with that of Hoffman et al. [11], who found that magpies use the LE to view a human approaching them from behind if their next behaviour was fleeing. Viewing prior to approach was low arousal (alert posture not adopted) and it used the RE. Withdrawal is therefore a behaviour that results from processing visual information in the RH, whereas approach follows processing by the LH. This specialization of the hemispheres for approach and withdrawal has been noted in other species, even in humans. For example, in humans the RH expresses negative emotions such as fear and aggression, as well as withdrawal, whereas the LH expresses positive emotions and approach [5]. The results obtained on withdrawal and approach behaviour of magpies are, therefore, consistent with established findings.

Jumping and pecking are agonistic behaviours, identified as part of the mobbing response towards predators and often involving physical contact with the predator [27]. Although circling does not involve physical contact, it is still generally associated with mobbing behaviour and perhaps the congregation of animals around a predator may be somewhat agonistic [3]. Research on other species has established that the RH is dominant for agonistic responses (summarised by [19]): e.g. chicks [30], toads [18,31] and the *Anolis* lizard [6] all strike preferentially at conspecifics on their left

side. Hence, the strong LE/RH bias that the magpies demonstrated in our study provides more evidence that the RH controls agonistic behaviour. Furthermore, our result demonstrates that the agonistic behaviours controlled by the RH are directed not only at conspecifics but also at a potential predator.

The LE/RH was also used when viewing the lizard in a high alert posture during inspection-only tests, when high arousal levels are indicated by the extended neck posture. This finding is consistent with the earlier research on chicks showing that viewing an overhead predator with the LE elicits more distress calls than viewing it with the RE [7]. Chicks also use the LE to examine novel objects [22] and the details of a stimulus: the LE detects small changes in familiar stimuli, whereas the RE detects large changes that represent categories rather than details [29]. Hence, it is possible that the magpies viewed the lizard merely as a novel stimulus, rather than a predator *per se*. However, this is unlikely since their responses to the taxidermic lizard were similar to those recorded when magpies detected wild lace monitors and other predators (Koboroff and Kaplan, in preparation) and the majority of presentations of the lizard involved mobbing behaviour (16 of the 22 tests), which is a typical response to predators and not novel stimuli [4]. This suggests that, when the magpies adopted the alert posture and viewed the lizard using the LE, they were doing so to examine the potential predator in more detail. We think that it is most likely that the magpies were viewing the lizard with the LE to process the details of the stimulus and assess whether this potential predator was a threat. This contrasts to a RE preference before approaching the predator, as mentioned above, and this RE use differed from LE viewing in that the birds did not adopt the high arousal posture. In other words, there are two types of viewing the predator: LE high alert and RE low arousal followed by approach.

The lack of bias in alert viewing during mobbing is intriguing since mobbing is primarily an agonistic response and yet no LE/RH bias was observed. The lack of bias may indicate a balance between approach and withdrawal and, hence, continuous assessment with the LE (withdrawal) and RE (approach). Use of the monocular fields of both the LE and RE would also ensure that both small and large (category) changes are detected.

Our results confirm existing data from laboratory studies and extend these to behaviour in the natural environment. The RH hemisphere appears to control most aspects of predator–prey interactions, from detection [30] through to mobbing and high alert inspection behaviour. Even withdrawal/escape from the predator is controlled by the RH in magpies, as in other species [14,15]. The evolutionary implications of the relationship between RH and predator–prey interactions suggest that a suite of anti-predator strategies may have been organized within the RH. Approach to the predator is the exception: approach follows use of the RE/LH and does not involve high alert. As shown in chicks, the RE/LH is used to focus attention on the cues that indicate large (category) differences between stimuli [20,29], which suggests that magpies may be approaching in order to examine the stimulus more closely. This interpretation is supported by the fact that such approaches were not followed by mobbing or agonistic interactions with the predator. The counterbalanced specialization of the LH for approach and the RH for withdrawal is notable given that the same specialization occurs in humans [5].

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