

Behavioural lateralisation in the Australian magpie (*Gymnorhina tibicen*)

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In many vertebrates, the brain is lateralised such that each hemisphere is specialised to serve specific functions. This may translate into lateralisation in behaviour through preferential use of receptors or appendages associated with a particular hemisphere (e.g., handedness) or in differential responses to stimuli perceived on the animal's left or right side. In this study, we investigated behavioural laterality in the Australian magpie, *Gymnorhina tibicen*. We found that, while the birds did not have a population bias for one antipredator behaviour (visual inspection of an approaching human), there were biases for another (alarm calling); those birds that used their left eye more relative to their right eye gave alarm calls more frequently. We also observed that juvenile birds begged for food on the right side of parents significantly more frequently than on the left side. These trends are consistent with trends in behavioural laterality that have been recorded in captive and lab-reared species. Ours is one of the few studies to observe patterns of laterality in a wild species.

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Brain lateralisation exists as a general pattern of differential perception and processing of stimuli and differential motor control associated with either hemisphere of the brain (Andrew & Rogers, 2002; Rogers, 2002). Lateralisation has been found in many vertebrate species and is common across multiple taxa (reviewed in Bisazza, Rogers, & Vallortigara, 1998). This phenomenon is exhibited at multiple levels, including laterality in neural structures and functions, peripheral systems, and behaviour (Vallortigara, Rogers, & Bisazza, 1999). Behavioural laterality is seen as a side preference in specific behaviours or a differential response towards stimuli presented in either lateral hemifield; these effects may be derived from peripheral lateralisation, neural lateralisation, or both.

Numerous techniques have been developed to look for evidence of laterality in behaviour in the laboratory. Several researchers have used a detour task to show a turning bias in poeciliid fish (e.g., Bisazza, Pignatti, & Vallortigara, 1997). Other studies have demonstrated patterns of laterality in social situations either by placing animals in a social decision task (McKenzie, Andrew, & Jones, 1998) or by simulating a social situation (Bisazza, De Santi, Bonso, & Sovrano, 2002; Bisazza, De Santi, & Vallortigara, 1999). Monocular testing (e.g., Rogers, 1997), assessment of eye preference (e.g., Dharmaretnam & Andrew, 1994), and dual-attention tasks (Rogers, 2000; Rogers, Zucca, & Vallortigara, 2004) have also been used to shed some light on the effects and functions of laterality.

These studies have revealed certain patterns that appear to be common across numerous taxa. Intense emotional responses, such as fear, are generally activated by the right hemisphere of the brain and inhibited by the left hemisphere (Andrew & Rogers, 2002). The right hemisphere of the brain is also associated with attending to the details of a stimulus and may be involved in processing input from topographic information (visual navigation, e.g., Kahn & Bingman, 2004; the reverse has been found in olfactory navigation, Gagliardo, Odetti, Ioale, Pecchia, & Vallortigara, 2005), whereas the left hemisphere categorises stimuli and controls motor responses that require fine manipulation (summarised in Rogers, 2002).

Laterality may benefit an organism by allowing concurrent attention on two different tasks. For example, Rogers et al. (2004) found that chicks, *Gallus gallus domesticus*, that had been incubated in dark environments (and thus had non-lateralised brains, Rogers, 1990) performed more poorly on and had poorer retention of a dual-attention task, as compared to lateralised chicks.

Despite all of the recent work on laterality, relatively few studies have attempted to demonstrate behavioural laterality in wild non-primates outside laboratory conditions. Typically, these types of studies have been designed to determine how patterns found in the laboratory might affect natural behaviour or whether patterns of differential response to stimuli on a lateral hemifield match those that have been found in the laboratory. For example, Franklin and Lima (2001) looked at laterality in a dual-attention task and found that two species of

sparrows had a favoured eye in vigilance behaviour, but that the two species differed in eye preference. Ventolini, Ferrero, Sponza, Chiesa, Zucca, and Vallortigara (2005) observed black-winged stilts in the wild, and determined that the birds preferentially used their right eye in predation and were more successful when they did so, and that they performed a number of sexual behaviours with a left-side bias. Extensive research has been done regarding lateralised tool manufacture and use by New Caledonian crows, *Corvus moneduloides* (e.g., Hunt, 2000; Hunt, Corballis, & Gray, 2001; Hunt & Gray, 2004; Rutledge & Hunt, 2004). Crows were found to have a strong population-level bias for using the right eye in manufacture, even in cases in which using the right eye would make the procedure more difficult (Hunt et al., 2001).

The present research is a study of lateralised behaviours in the Australian magpie, *Gymnorhina tibicen*, in a semi-rural area of eastern Australia. Australian magpies are territorial ground-feeding birds found in rural, suburban, and urban areas throughout Australia (Slater, Slater, & Slater, 1994) and are an ideal species for study because their method of foraging makes them quite accessible to observation and minimal manipulation. Magpies perform what E. D. Brown and Veltman (1987) refer to as “walk foraging”, wherein they alternately walk a few steps and pause for a second or two before probing the ground in search of soil invertebrates. During the post-fledging period, juveniles follow foraging adults and beg for food. We chose to investigate laterality in antipredator responses, including eye use when viewing an approaching human and alarm calling, and in begging behaviour, as both of these are situations with which wild species must contend on a daily basis.

LATERALITY IN ANTIPREDATOR RESPONSE AND FEAR BEHAVIOUR

Antipredator behaviour can be a major determinant of survival and thus directly affects fitness. If one hemisphere of the brain is specialised for the detection of predators, animals should preferentially use the corresponding peripheral systems (primarily auditory and visual systems in birds). A number of prior studies indicate that animals have population-level biases to respond more readily to predators seen in their left monocular field of vision, as seen in adult chickens (Evans, Evans, & Marler, 1993) and young chicks (Rogers, 2000), as well as in toads (Lippolis, Bisazza, Rogers, & Vallortigara, 2002) and dunnarts (Lippolis, Westman, McAllan, & Rogers, 2005). In fish, preferred use of an eye has been reported for predator inspection (Bisazza, Facchin, Pignatti, & Vallortigara, 1998; De Santi, Sovrano, Bisazza, & Vallortigara, 2001; C. Brown, Gardner, & Braithwaite, 2004) though the direction of that bias appears to vary by taxon (Bisazza et al., 1997).

As a proxy for antipredator behaviour, we observed magpies' responses to an approaching human. We predicted that if an approaching human were viewed as

a threat by magpies, they would preferentially use their left eye when viewing the human (Andrew & Rogers, 2002).

Fear responses have also typically been found to be lateralised, with the right hemisphere being associated with stronger responses (Andrew & Rogers, 2002). *G. tibicen* has a rich variety of calls and complex song patterns (Kaplan, 1999) including easily identifiable alarm calls (E. D. Brown & Farabaugh, 1991), which are elicited at variable intervals in the presence of an intruder or predator. Since alarm calling is likely to be associated with fear, we predicted that there would be a correlation between alarm calling in response to human incursion and left eye / right hemisphere use.

LATERALITY IN BEGGING

After fledging, juvenile magpies are fed by both parents for a number of weeks. When begging, a juvenile follows an adult foraging on the ground, running whenever the adult pauses. It moves very close to the adult (within a few centimetres) on one side or the other while making a loud shrill begging call, continuing the call until the adult either feeds or “scolds” the young bird (Roberts, 1963).

We observed parent–offspring pairs in the wild to determine if juveniles had a tendency to approach on the right or the left side of parents. We expected that juveniles would prefer to use their left eye to view parents as they approached, and thus would approach on the right side of parents. A similar trend has been reported for domestic chicks (Dharmaretnam & Andrew, 1994); chicks approached an object upon which they had imprinted using their left eye preferentially.

GENERAL METHOD

We observed 43 magpies (13 females, 22 males, and 8 juveniles) within the University of New England campus in Armidale, NSW, Australia. All of these birds were well habituated to the presence of humans. Individuals were assigned unique identification numbers, according to age and sex, and could be easily identified by distinctive patterns on their wings and back (Slater et al., 1994). Age (hatch year or after-hatch year) and sex were determined by observation of the plumage; females and juveniles have a grey plumage on the back of their neck, whereas males have a white plumage, and juveniles have plumage with flecks of grey on the breast and dark grey beaks as opposed to light grey with a dark tip in adults. All data were collected from early November to mid December 2000 by the first author.

For both experiments, relative dominance scores were computed for each individual by the formula $(R-L)/(R+L)$, where R is the number of right observations and L is the number of left observations. Significance of individual side biases were evaluated by treating sequences of left and right scores as a set of

binomial data and calculating a z -score, which is normally distributed for sufficient sample sizes (Zar, 1996). Population biases were evaluated through paired t -tests, treating the number of left and right scores as independent pairs of data points (Hunt et al., 2001). Experiment 1 required further statistical analyses, which are described in the results and discussion section.

EXPERIMENT 1: ANTIPREDATOR RESPONSE AND FEAR BEHAVIOUR

Our first study was an investigation of laterality in fear and antipredator behaviour. Antipredator response is a rich area in which to study the occurrence of behavioural lateralisation, as it may have a direct effect on fitness. We used an approaching human to stimulate antipredator behaviour in magpies. The birds' responses to human approach were similar to reported antipredator behaviours (E. D. Brown & Veltman, 1987). Specifically, when approached by a human, the magpies typically responded by running short distances (1–3 metres) directly away from the human. As in most birds, the binocular field is rather limited in magpies, due to lateral placement of eyes. Inspection of the human therefore required that the magpies turn their heads to use either their left or right monocular field. Other responses included alarm calling or flying away.

Method

The tester approached individual magpies from behind, usually when they were foraging, at a constant slow walking pace (~ 1.5 m/s) to within two or three metres. Once a bird had responded to the tester's presence, the tester continued to follow that bird in this manner until the bird flew away or became obscured (e.g., by entering cover). Throughout this period, the tester noted which eye the bird used each time it turned its head to watch him and also noted any alarm calls given. Data were thus recorded as a sequence of left and right glances and alarm calls.

Results and discussion

We collected data from 36 magpies. Of these, 28 provided sufficient data for an estimation of side bias (more than five scores each of both left and right glances; Zar, 1996). The tester recorded between 10 and 44 scores per individual (mean number of scores $\pm SE$: 23.1 ± 1.43). Five birds showed a side preference significant at $\alpha = 0.05$ ($z \geq \pm 1.96$). Two of these birds preferred to use their left eye more, and three favoured their right eye. There was no population-level lateralisation in eye preference for viewing an approaching human, paired t -test, $t = 0.222$, two-tailed $p = 0.826$, $n = 28$ (Figure 1).

We should note that these data do not reflect only the initial detection of the threat, but subsequent glances as well. Initial detection of a predator is probably

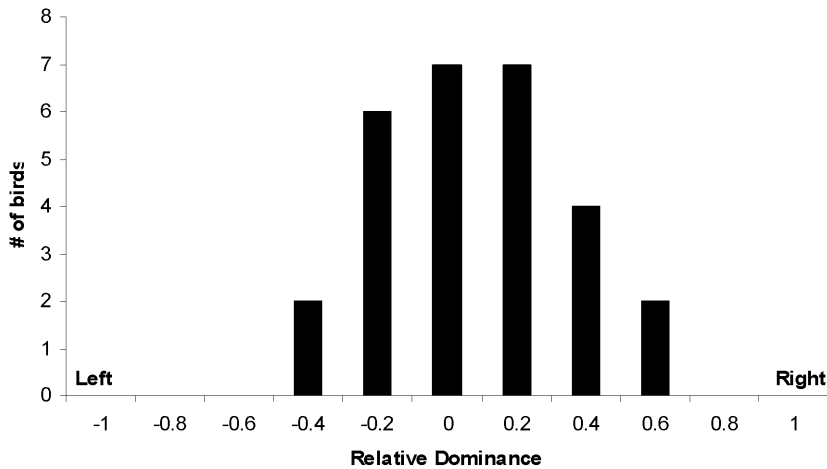


Figure 1. Histogram of relative dominance scores for magpies viewing a human. Higher relative dominance scores indicate increasing relative use of right eye. A total of 23 birds (82%) showed no significant preference, 2 (7%) preferred their left eye, and 3 (11%) preferred their right eye.

more important than monitoring a predator that has already been detected, and thus one might expect to see stronger lateral biases (i.e., more left eye glances) in the first glance only. This was not the case, however; 15 birds (42%) glanced left initially, while 21 birds (58%) glanced with the right eye first, binomial test, $z = 1.00$, $p = 0.317$. Perhaps the lack of a bias in this behaviour reflects the birds' readiness to face hazards, which occur essentially at random in the animals' environment; danger could approach as easily from the bird's left side as from its right, and it could be detrimental to have a reduced ability to detect threats coming from one side.

A total of 18 birds (50%) gave between 1 and 17 alarm calls (mean number of calls \pm SE: 4.89 ± 1.00) when approached. Since we had a different number of scores (right and left eye glances) for each individual, we were concerned that the number of calls recorded would need to be corrected for sampling effort in analyses of fear response. Thus, we ran regression of calls on sample size. The number of calls given was not a function of sampling effort (i.e., the number of calls given was independent of the total number of glances recorded, $R^2 = 0.00905$, $F_{1,16} = 0.146$, $p = .707$).

To test if fear responses were correlated with eye preferences, we ran a robust regression of calls on relative eye dominance. This method is similar to a linear regression, but it uses maximum likelihood to assign a weight to each point used in the estimation of slope (Markatou, Basu, & Lindsay, 1998). Thus this method provides a more accurate estimate of slope than standard regression, by reducing the effects of outliers, but is more conservative than removing outliers

altogether. Of the birds that gave alarm calls, those that used their left eye more also tended to give more alarm calls, $F_{1,14.25} = 4.55$, $p = .0543$. The robust regression weighted one point at 0.075 (Figure 2, light grey), three other points between 0.8 and 0.85 (Figure 2, dark grey points), and all other points at between 0.95 and 1.0. A standard regression (included for comparison only, Figure 2, grey line) found a similar trend, $F_{1,16} = 4.82$, $p = .0433$. Birds also called more if their initial glance was with the left eye, t -test, $t = 2.61$, $df = 16$, $p = .0189$.

We evaluated sequence effects of alarm calls with a chi-squared test to determine if calls were more likely to follow a left eye glance or a right eye glance. Birds were significantly more likely to give alarm calls immediately following a left glance, $\chi^2 = 28.0$, $df = 16$, $p = .0320$. Subjects gave 1.83 times more alarm calls following a left eye glance than a right eye glance.

These results suggest that, while the birds generally had no eye preference for viewing an approaching threat, their response to the threat differed according to which eye they were using. Birds were more alarmed by the presence of the tester if they were using their left eye more, both initially and throughout the observer's approach. This is consistent with a general trend of left eye / right

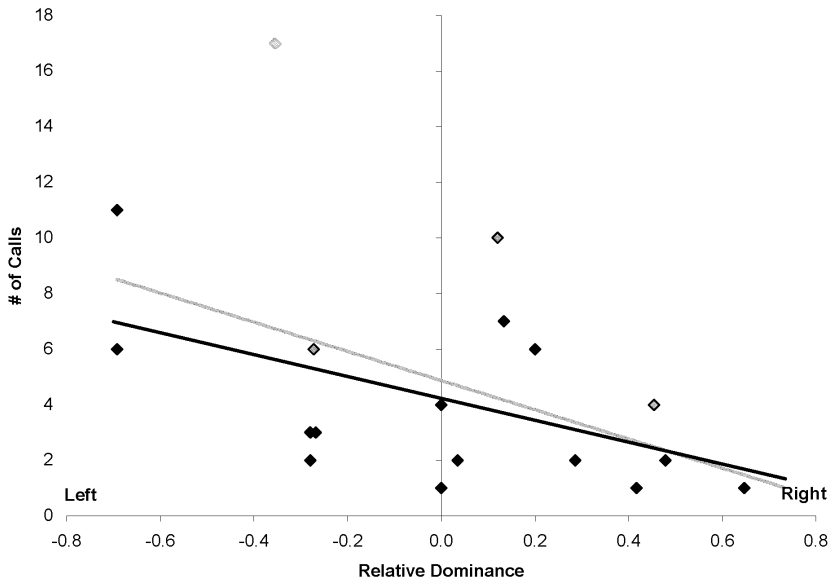


Figure 2. Number of alarm calls given as a function of relative dominance. Calling birds that used their left eye proportionally more gave more alarm calls: black line, $\text{Calls} = -3.94 * (\text{Rel. Dom.}) + 4.24$, $R^2 = 0.236$, $F_{1,14.25} = 4.55$, $p = .0543$. One point (light grey) was weighted to 0.075, and three others (dark grey) were weighted between 0.8 and 0.85. A standard regression is provided for comparison: grey line, $\text{Calls} = -5.25 * (\text{Rel. Dom.}) + 4.87$, $R^2 = 0.231$, $F_{1,16} = 4.82$, $p = .0433$.

hemisphere use in fear responses that has been reported in numerous taxa (Andrew & Rogers, 2002). This may be a demonstration of how an animal's response to stimuli in its environment may depend in part on which side of the animal the stimulus occurs. Other naturalistic studies have shown effects of the side of stimulus presentation on response intensity. For example, Hews and colleagues have found that the intensity of aggressive response in lizards was significantly higher when offending conspecifics were initially in the left visual field (Hews, Castellano, & Hara, 2004; Hews & Worthington, 2001).

In the present research, while the same information (presence of a threat) presumably reaches the bird's brain regardless of which eye the bird uses, it may be that specialised processing that occurs in one hemisphere of the brain elicits a different response to threats perceived by the left eye than those seen by the right eye.

EXPERIMENT 2: BEGGING

Our second experiment was an investigation of lateralisation of begging behaviour in juvenile magpies.

Method

From a distance sufficient to avoid disturbing the birds (> 5 m) or from behind a blind, the observer watched six parent–juvenile pairs foraging. Each time the juvenile came to within about 10 cm of the parent while making a begging call, the observer noted which side of the parent the juvenile approached. Behaviours received a score only if the juvenile had been separated from the adult by at least two bird-lengths (about 25 cm) before approaching to beg. Between 16 and 64 scores were obtained per individual (mean number of scores \pm *SE* = 35.2 \pm 8.10).

Results and discussion

Six juveniles were observed begging adults for food. Five (80%) of these birds begged significantly ($p < .05$) more on the right side of adult birds than on the left (Table 1). There was a highly significant group-level bias for begging on the right side of parents, paired *t*-test, $t = 4.08$, two-tailed $p < .01$, $n = 6$. Juveniles were 2.46 times more likely to beg on the right side than on the left.

By begging on the right side of a parent, a juvenile uses its left eye to view the adult and is in the right eye field of view of the parent. A preference for the right side could result from laterality in the juvenile, the adult, or both. We offer a number of non-exclusive hypotheses for this finding.

In juvenile birds, prior studies have reported a preference for keeping familiar stimuli in the left eye field of view (e.g., Dharmaretnam & Andrew, 1994; McKenzie et al., 1998), and other studies have found a similar preference in

TABLE 1
 Laterality in begging behaviour

	<i>Subject ID</i>					
	<i>2j2</i>	<i>2j3</i>	<i>3j1</i>	<i>3j2</i>	<i>3j3</i>	<i>3j4</i>
Left Side	24	13	5	9	6	4
Right Side	40	43	24	15	16	12
Rel. Dom.	0.25	0.5357	0.655	0.25	0.455	0.5
<i>p</i>	.0455	< .0001	.00416	.222	.0332	.0455

All six juvenile subjects begged more on the right side of the parent than on the left and this trend was significant in five of these subjects ($p < .05$). Overall there was a strong group bias for begging on the right side of parents, paired *t*-test, $t = 4.08$, two-tailed $p < .01$, $n = 6$.

other taxa (great apes: Hopkins, 2004; fish: Bisazza et al., 1999; anurans: Bisazza et al., 2002). This preference is thought to result from patterns of brain lateralisation, wherein the right hemisphere is specialised for detailed perception of stimuli and thus determining identity of conspecifics (Andrew & Rogers, 2002; Vallortigara & Andrew, 1994). Thus, perhaps the juveniles in this study approached on the right side of the parent so as to keep parents in their left eye field of view.

Another possibility is that by approaching on the right side, juveniles evoke less aggression from parents. The left hemisphere is known to inhibit conspecific aggression in chickens (Vallortigara, Cozzutti, Tommasi, & Rogers, 2001), lizards (Hews et al., 2004; Hews & Worthington, 2001), and toads (Robins, Lippolis, Bisazza, Vallortigara, & Rogers, 1998). By approaching in the right hemifield, a juvenile magpie may avoid being scolded.

The observed trends could also be a result of an adult preference for keeping juveniles on the right side. Adults are capable of manipulating juvenile behaviour by feeding juveniles that approach on one side preferentially to those that approach on the other. Juvenile preference thus may be at least partially a result of differential feeding. Adult side preference may be due to specialisation in the left hemisphere/right eye system for precise motor control, such as might be required when feeding offspring (Andrew, Tommasi, & Ford, 2000; Rogers, 2002).

Very little research has been done on laterality in fledgling feeding behaviours. Many of the hypotheses we have proposed could be tested with relative ease. For example, one could reasonably predict that if juveniles must learn that they will be fed more frequently on the right side of a parent, there would be an increase in the tendency to beg on the right side over time.

GENERAL DISCUSSION

Our data demonstrate that visually guided behavioural lateralisation can be assessed in the natural activities of a wild avian species using direct observation and minimal manipulation. This is the first study to report behavioural lateralisation in Australian magpies (although subsequent research by Rogers and Kaplan (2005) has shown that they use the left eye preferentially to scan overhead for aerial predators) and one of very few studies whose specific aims were to assess behavioural lateralisation in a bird in its natural environment.

It should be noted that, although the lateralised behaviour reported here most likely results from lateralisation at the level of the forebrain, some contribution could come from lateralisation of peripheral systems. For example, European starlings (*Sturnus vulgaris*) have been shown to have lateralised discrimination ability (Templeton & Gonzalez, 2004) which may be consistent with a differential distribution of retinal receptors (Hart, Partridge, & Cuthill, 2000). Unfortunately, we have no information on the distribution of retinal receptors in *G. tibicen*.

Like many studies of behaviour in a natural environment, this study leaves us with more questions than answers. Are birds using their left eye really more fearful, or are they more prone to alert conspecifics when using the left eye? Would they respond in a similar manner to an actual predator? Is right side begging a consequence of juvenile preference for viewing parents with the left eye (or external stimuli with the right), or a result of differential rewarding on the right side? In either case, how does this behaviour benefit the animals, and how did it evolve? Detailed studies of laterality often require precision that can be achieved only in artificial environments, but more studies like this one will be necessary to learn how the phenomenon affects an animal in the natural world.

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