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Animal behaviour

Mimicry-dependent lateralization in the visual inspection of foreign eggs by American robins

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Brain lateralization, or the specialization of function in the left versus right brain hemispheres, has been found in a variety of lineages in contexts ranging from foraging to social and sexual behaviours, including the recognition of conspecific social partners. Here we studied whether the recognition and rejection of avian brood parasitic eggs, another context for species recognition, may also involve lateralized visual processing. We focused on American robins (*Turdus migratorius*), an egg-rejecter host to occasional brood parasitism by brown-headed cowbirds (*Molothrus ater*) and tested if robins preferentially used one visual hemifield over the other to inspect mimetic versus non-mimetic model eggs. At the population level, robins showed a significantly lateralized absolute eyedness index (EI) when viewing mimetic model eggs, but individuals varied in left versus right visual hemifield preference. By contrast, absolute EI was significantly lower when viewing non-mimetic eggs. We also found that robins with more lateralized eye usage rejected model eggs at higher rates. We suggest that the inspection and recognition of foreign eggs represent a specialized and lateralized context of species recognition in this and perhaps in other egg-rejecter hosts of brood parasites.

1. Introduction

Cerebral lateralization, first studied in detail over 150 years ago and thought to be exclusive to humans until only around 25 years ago, has since been described in a diversity of vertebrate and invertebrate lineages [1–5]. Left or right eye and appendage use biases commonly appear in natural behaviours including foraging, prey discrimination, predator detection, agonistic responses and courtship and mating [1] (table 1). Sidedness can differ in separate contexts for the same individual and these biases are also not always shared between individuals of the same species [14]. Thus, although the term ‘lateralization’ is used to describe side-based biases in function at the individual, population and species level, these biases might have evolved independently and convergently [14]. Understanding the presence and variation in lateralized behaviours at multiple levels can give a clearer picture of its adaptive functions and evolutionary pathways.

The lateralization of visual inspection has been studied extensively in a variety of social contexts relating to species recognition, but it has yet to be studied in the context of host responses to avian brood parasitism, where both population- and individual-level variation exists in parasite-rejection decisions. For hosts, the acceptance of foreign eggs is costly, as brood parasitism can result in a lower hatching rate, decreased nestling growth and increased nestling

Table 1. Non-exhaustive, representative classification of lateralization in a range of taxa and biological contexts, illustrating the conceptual organization of laterality patterns in nature. Lateralization in eye and hand/paw use is shown at the individual, population and inter-population levels.

Species	behavioural context	outcome	reference
individual			
common octopus (<i>Octopus vulgaris</i>)	predatory	left (5 individuals) or right (3 individuals) eye preference when looking at a crab model	[6]
Campbell's monkeys (<i>Cercopithecus c. campbelli</i>)	foraging	left (6 individuals) or right (8 individuals) eye preference looking through a tube at a seed	[7]
New Caledonian crow (<i>Corvus moneduloides</i>)	foraging	stick tool use to left (2 individuals) or right (2 individuals) of head while foraging	[8]
population			
black-winged stilt (<i>Himantopus himantopus</i>)	predatory and sexual	majority of right eye use for predatory pecking and majority of courtship displays when female was seen with left visual hemifield	[9]
Australian green tree frog (<i>Litoria caerulea</i>)	agonistic	majority of strikes per frog when competitor is in left visual hemifield	[10]
honeybee (<i>Apis mellifera</i>)	foraging	bees entering an open cavity have a strong rightward turning bias but no bias when entering a sequential choice maze	[11]
domestic chick (<i>Gallus gallus domesticus</i>)	social recognition	chicks using the left eye discriminate between stranger and companion better than chicks using the right eye	[12]
inter-population			
poeciliid spp. (<i>Brachyraphis episcopi</i>)	anti-predator vigilance	fish from high predation regions preferred right eye to view a live predator, whereas fish from low predation regions had no preference	[13]

and fledgling mortality [15–18]. American robins (*Turdus migratorius*; hereafter robin), an occasional host of the brown-headed cowbird (*Molothrus ater*; hereafter: cowbird), are rejecters of most cowbird eggs and thereby eliminate the recoverable costs of brood parasitism [19,20]. Previous experiments using various model egg colours produced extensive variability in the rejection behaviours by robins, and these responses were highly repeatable within individuals [21]. Therefore, robins are an ideal species to study the proximate basis of the potentially lateralized assessment and discrimination of parasitic eggs.

To determine how robins make their egg-rejection decisions, the process of visual clutch inspection must be understood. Ground foraging birds, like the American robin, tend to have a single centre of acute vision (i.e. fovea) in each eye that projects laterally given the positioning of the eyes in the skull [22]. This centre of acute vision has the highest densities of cone photoreceptors involved in colour vision [23]. In birds, the right eye is often preferred for visual discrimination in foraging tasks, whereas the left eye is used for viewing familiar conspecifics [24–32]. Few studies have investigated lateralization in avian colour discrimination, but in conditioning experiments, the right visual hemifield, and therefore left brain hemisphere, has been shown to be typically dominant [33,34]. Furthermore, in vertebrates, the left brain hemisphere is preferentially involved in focused attention to repeated stimuli and is important in categorization, while the right hemisphere is characterized by responding to novelty and is important in processing stress cues [1]. Robins can respond to multiple features of foreign eggs in their rejection decisions, including background colour, size and maculation

[35], which could favour the use of the right eye. However, non-mimetic parasitic eggs are a known physiological stressor for hosts of avian brood parasites [36], which could predict the biased use of the left eye for rejection responses. Here, we investigate whether lateralized eye use is present in robins when examining mimetic and non-mimetic model eggs in the nest.

2. Material and methods

(a) Experiments

We conducted this experiment during May and June of 2017 and 2018, using a total of 26 American robin nests in ornamental tree farms, apple orchards and suburban backyards around Urbana, Illinois. All nests used were active at the incubation stage and had a natural clutch size of at least three eggs. For experimental parasitism, we purchased commercially three-dimensional printed eggs (Model no: Cow Bird; Shapeways.com) in the size and shape of brown-headed cowbird eggs and painted robin-mimetic blue or cowbird-like white ground colours (for manufacture and painting details, see [37]).

In 2017, either an immaculate blue or white egg was placed into an active robin nest [37] and recorded with a GoPro Hero Camera (Los Angeles, USA) until its maximal battery life on a single charge. The camera was secured above the nest and set up on a camouflaged extended flexible gooseneck and wrapped around a nearby branch, ideally positioned 20–80 cm away from the nest with the clamp of the gooseneck latched to a nearby branch, depending on the environment. In 2018, each active robin nest received both a blue and white egg added to their natural clutch for consecutive 1-h trials (one egg at a time), in a

Figure 1. (a) Median and quartiles for difference in absolute eyedness index [ABS(EI)] in robins when observing a mimetic egg and when observing a non-mimetic egg ($p = 0.004$). (b) Median and quartiles for difference in ABS(EI) in robins when they accepted the experimentally added egg and when they rejected it ($p = 0.005$). (Online version in colour.)

randomized order. The 2018 nests were recorded simultaneously with two custom cameras (Sony 1.8 mm high-definition cameras connected to a Brandoo two-channel digital video recorder) placed on either side of the nest to gain more angles at the returning and incubating female robin.

All videos were reviewed and the number and direction of each head orientation towards the nest for every visit by a robin were recorded and categorized as either a left or a right head tilt when discernible. These head tilts were counted only when the robin was looking primarily with one eye down at the nest, from the time a robin stood on the edge of the nest until it either (1) rejected the egg, (2) began incubating or (3) flew off. For the trials in which two cameras were on either side of the nest, the numbers of left and right head tilts observed from both videos were averaged to minimize bias from the camera angle. In robins, only females incubate the eggs [38] and so our observed head tilts counted should represent maternal behaviours. To assess the replicability of our methods, all the videos were viewed and scored separately by two people (H.M.S. and K.S.).

(b) Statistical analysis

We used two indices to characterize eye bias for each nest. An eyedness index (EI, range: -1 to 1) was calculated using the formula: $(R - L)/(R + L)$, with R representing the number of right head tilt counts per video recording, and L representing the number of left head tilts [7]. Negative values indicate a bias towards left eye use, while positive values indicate a bias towards right eye use. A second index is the absolute value of EI [ABS(EI)], which is used to characterize the strength but not the direction of the side bias [7].

To determine the repeatability of observations between the two observers, two-tailed paired Spearman's rank correlations were used for both the total number of head tilts counted and the EI calculated by the observers. To assess whether there was an effect of video types between years, general linear mixed models (GLMM) were used for the number of head tilts and the EI metric, with the nest ID as a random effect. To determine if EI and ABS(EI) biases were present when robins examined blue (mimetic) or white (non-mimetic) eggs, one-sample Wilcoxon tests were used (with the random expectation of 0). GLMMs with nest ID as a random effect were used to assess the effect of treatment type on EI, ABS(EI) and total number of head tilts, as well as the effect of the number of head tilts on ABS(EI). Finally, GLMMs with nest ID as a random effect were used to assess the effect of EI, ABS(EI), and number of head

tilts on whether the egg was accepted or rejected in 2018, while accounting for treatment effects. JMP 12.0.0 (SAS Institute Inc., Cary, NC) was used to analyse linear mixed models, and R v. 3.5.1 was used for non-parametric tests and figures.

3. Results

We found positive interobserver repeatability for the number of head tilt counts recorded ($\rho = 0.87$, $p < 0.0001$) and for the calculated EI metric ($\rho = 0.50$, $p = 0.01$). In addition, there was no statistical difference between 2017 (single camera footage, $n = 15$ nests) and 2018 (double camera footage, $n = 12$ nests) in either the head tilt counts detected ($F_{1,22} = 1.05$, $p = 0.32$) or in the calculated EI metric ($F_{1,20} = 0.79$, $p = 0.39$).

When viewing mimetic eggs, robins had a lateralized bias in eye use, as shown by ABS(EI) ($\mu = 0.86$, $W_z = -1.80$, $p = 0.036$). However, the direction of this bias varied at the nest level and was not significantly skewed towards either the left or right eye preference overall in the population, as shown by the unbiased EI metric ($\mu = -0.12$, $W_z = 1.22$, $p = 0.89$). By contrast, when viewing non-mimetic eggs, robins did not show lateralized eye use, as indicated by both the ABS(EI) ($\mu = 0.45$, $W_z = -1.34$, $p = 0.09$) and the EI metrics ($\mu = 0.21$, $W_z = 0.70$, $p = 0.76$). There was no significant difference in EI when robins inspected mimetic versus non-mimetic eggs ($F_{1,4} = 0.67$, $p = 0.46$), whereas ABS(EI) shifted from more lateralized to less biased scores when robins examined mimetic versus non-mimetic eggs ($F_{1,14} = 11.56$, $p = 0.004$) (figure 1).

We examined whether our analyses showed a stronger absolute lateralized bias when viewing eggs with fewer total head tilt counts. Overall, there was no significant difference in the number of head tilts that robins used when looking at mimetic versus non-mimetic eggs ($F_{1,10} = 1.65$, $p = 0.23$). However, there was a negative relationship of the number of head tilts on ABS(EI) ($F_{1,12} = 12.56$, $p = 0.042$). Yet, ABS(EI) was still significantly greater for mimetic versus non-mimetic model eggs ($F_{1,16} = 5.38$, $p = 0.034$), even when accounting for covariation with head tilt counts ($F_{1,13} = 7.24$, $p = 0.019$).

During the 1-h exposure of the paired-design 2018 experiments ($n = 12$ nests), non-mimetic eggs were rejected more often than mimetic eggs (8% mimetic eggs rejected versus 33% non-mimetic eggs rejected) ($\chi^2 = 4.5$, $p = 0.034$). In turn,

ABS(EI) was higher for nests in which experimental eggs were rejected versus nests where eggs were accepted ($\chi^2 = 7.8$, $p = 0.0052$), irrespective of the order in the stimulus presentation ($\chi^2 = 2.3$, $p = 0.13$) (figure 1).

4. Discussion

These results show that when robins examine an experimentally added mimetic egg in their nest, they apply a stronger bias to which eye they use to inspect that egg. By contrast, when robins inspect experimentally added non-mimetic eggs, they use both eyes in a more balanced way. This outcome was constant across the two different years of treatments in the study. Thus, the results are consistent with a context-dependent strategy for lateralized robin eye use when observing eggs in their nest. In addition, the increased rejection of eggs when eye-use bias was higher suggests that the lateralization of eye use may also affect the success of antiparasitic egg-rejection decisions in this host species. Population-level eye-use lateralization biases reported here have also been found in other social recognition contexts: for example, domestic chicks (*Gallus domesticus*), adult hens and Japanese quail (*Coturnix japonica*) are better at discriminating familiar individuals from unfamiliar individuals with their left eye [26,28–31,39].

The recognition and rejection of brood parasitic eggs can be considered a type of species recognition, in which birds must distinguish between their own eggs and the eggs of heterospecifics. However, the elimination of a parasitic egg could also be considered an agonistic response [36]. Similar to social recognition, aggressive responses are usually more frequent when the stimulus is viewed with the left eye, as has been found in toads [10], lizards [40] and birds [41], although all in the context of aggression towards conspecifics.

In our study, the stronger bias in lateralized eye use when examining mimetic eggs was not due to consistent use of the left or right eye across the population, but rather strong bias at the nest level with interindividual variability in which eye is preferred. Directional asymmetries occurring at the individual level, also known as antisymmetry, are hypothesized to occur to increase brain efficiency [1]. Population-level lateralization has been hypothesized to occur as a result of interindividual interaction, in which individuals must align their asymmetries with other individuals in the group [42]. When viewing eggs, however, robins do not have to coordinate their behaviour with other individuals, which might explain why there was no population-level trend in the

direction of eye-use bias in the context of nest visual exploration to discriminate brood parasite eggs.

Robins that rejected our model eggs were more biased in their eye use than accepters. It is possible that stronger lateralization in eye use can promote better discrimination between eggs and aid in more successful rejection decisions for hosts. In the domestic chick, strongly lateralized individuals are faster at detecting model predators and are better at distinguishing between grain and pebbles [43,44]. In parrots, strongly lateralized individuals performed better at problem-solving tasks using their eyes and feet than less lateralized individuals. [45]. The addition of non-mimetic eggs can be a physiological stressor for avian hosts, so it is possible that non-mimetic eggs are a source of stress for robins and that the shift in the laterality of eye use is mediated hormonally [36,46,47].

In sum, these experiments show that lateralization in the eye use of robins inspecting eggs is context-dependent, with changes in lateral bias according to the mimicry of a foreign egg. The patterns in eye-use sidedness reported here thus span multiple tiers of biological organization, with a population-level bias in the strength of lateralization and variation in individuals' left versus right preferences. More importantly, these eye-use biases have potential impacts on the rejection rates of brood parasitic eggs, with more highly lateralized individuals rejecting model eggs at higher rates. Consequently, it is conceivable that lateralization in eye use could contribute as an additional element in the coevolved defensive repertoire for hosts to aid in egg-rejection against avian brood parasites.

Ethics. All research was approved by University of Illinois IACUC no. 17049 and by federal, state and institutional agencies.

Data accessibility. Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.p1k2426> [48].

Authors' contributions. M.E.H., T.J.B. and E.F.-J. conceived the study, M.D. and M.E.H. performed the experiments, H.M.S. and K.S. analysed video footage, H.M.S. and M.E.H. performed statistical analysis, H.M.S. wrote the first draft; all other authors contributed to writing the final draft. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Competing interests. We declare we have no competing interests.

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