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Animal behaviour

European starlings recognize the location of robotic conspecific attention

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Looking where others are allocating attention can facilitate social interactions by providing information about objects or locations of interest. We asked whether European starlings follow the orientation behaviour of conspecifics owing to their highly gregarious behaviour. Starlings reoriented their attention to follow that of a robot around a barrier more often than when the robot's attention was directed elsewhere. This is the first empirical evidence of reorienting in response to conspecific attention in a songbird. Starlings may use this behaviour to obtain fine-tuned spatial information from conspecifics (e.g. direction of predator approach, spatial location of food patches), enhancing group cohesion.

1. Introduction

Humans are sensitive to the attentional states of others, particularly where each other is looking. Gaze direction (i.e. where the retinal centres of acute vision project into visual space) is thought to indicate where one's attention is, and can be used as a form of social information to facilitate detection of relevant stimuli, highlight social interactions and alert others to danger [1]. The ability to determine where someone's visual attention is directed is called *gaze sensitivity* [2]. Additionally, animals can *follow* the visual attention of others by reorienting their own gaze (i.e. gaze following [1]). Gaze following is often further divided into (1) following gaze into distant space and (2) following gaze around a barrier or geometric gaze following [2]. The latter is considered more cognitively complex because the gaze follower should estimate a line of sight around the barrier to a point in space it may not have visual access to from its current position [1].

For humans, determining the point of visual attention using the eyes alone has relatively low ambiguity because they have (i) frontally placed eyes that can be seen simultaneously, (ii) a single retinal centre of acute vision (i.e. fovea) per eye projecting to the same point in space (i.e. vergent visual axes) and (iii) white sclera indicating eye (and hence foveal) position. Humans can then use eye orientation to establish where individuals are directing visual attention (e.g. foveal projection). Interestingly, some animals that are sensitive to gaze direction have visual systems that are different from humans [2]. For example, many birds have laterally placed eyes with centres of acute vision projecting to two distinct points in space [3], which increases uncertainty about gaze direction [2]. Additionally, fixation in birds is different from that in humans, who generally lock their gaze on a given object. Birds appear to fixate by moving their heads sideways [4], which can result in exposing the centre of acute vision of each eye to a given object alternatingly. Thus, changes in the position of the head *over time* provide information about gaze in birds. Overall, species with laterally placed eyes likely use different cues for following the location of conspecifics' attention.

In this study, we assessed whether European starlings (*Sturnus vulgaris*) changed their attention in response to changes in the orientation behaviour of a robotic conspecific. We focused on manipulating visual cues indicative of visual attention because vision is highly spatially specific due to the image-forming nature of the eye [5]. We chose starlings because they use social information from conspecifics [6] and are sensitive to human visual attention [7]. Additionally, the starling visual system
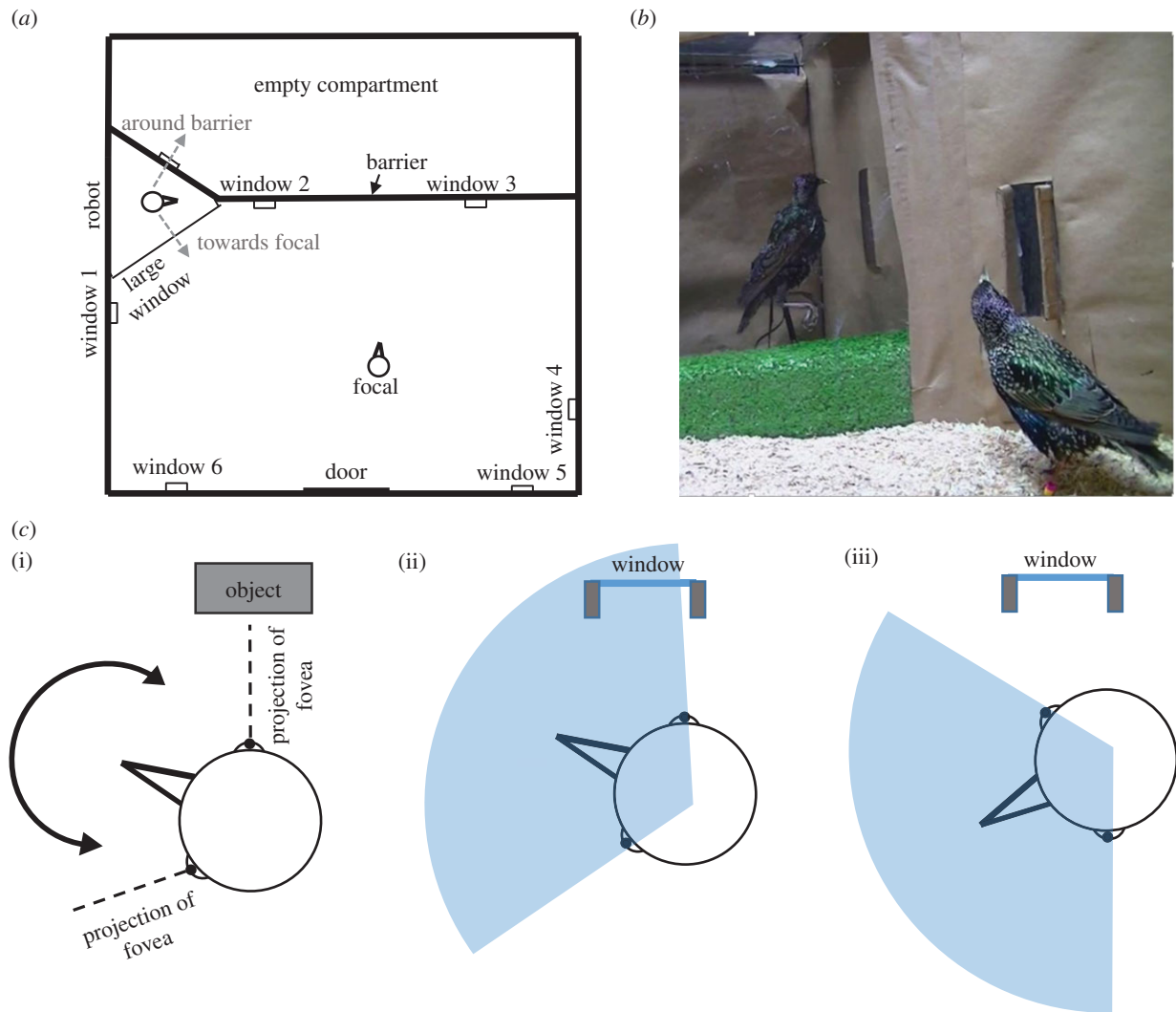
(a)

(b)

(c)

(i) (ii) (iii)

Figure 1. (a) Diagram of the experimental arena. (b) Starling orienting attention into the empty compartment during the around barrier treatment. (c) Using the visual system configuration of starlings, we determine the head positions where the animal had higher chances of projecting its centres of acute vision through the window (shaded area; details in the electronic supplementary material). (Online version in colour.)

has been characterized [3,8], which allowed us to develop methods to approximate the location of visual attention.

2. Material and methods

We conducted this experiment from September 2013 through January 2014 (details in the electronic supplementary material). Our experimental arena consisted of a three-compartment enclosure (figure 1a): an empty compartment, a compartment for the live bird (hereafter, focal) and a compartment for the robotic bird (hereafter, robot; figure 1a). Four small windows looked outside the enclosure while two were on the wall shared between the focal compartment and the empty compartment (hereafter, barrier), allowing the focal visual, but not physical, access to the empty compartment (figure 1b; electronic supplementary material). A large window allowed visual contact between the focal and the robot (figure 1a; electronic supplementary material). Additionally, there was a small window between the robot and the empty compartment (figure 1a; electronic supplementary material).

In our experimental paradigm, we manipulated the visual attention of the robot and measured changes in head and body orientation of a live bird. We intended to manipulate where the robot was looking based on information on the starling visual system [3,8]; however, we did not manipulate its behaviour with respect to other sensory modalities (e.g. hearing, olfaction). We used two strategies to overcome the problem of determining

where an animal with laterally placed eyes was directing its attention, both for the robot and the live bird. First, given the wide visual field (i.e. the space around the head that an animal can see) of starlings, we restricted the visualization of the empty compartment by covering all the enclosure walls with cardboard except for the windows. This allowed us to use more conservative criteria in terms of head positions that would indicate animals focusing their attention in a particular direction. Second, to establish the range of head positions indicating the direction of attention, we took into consideration the retinal and visual field configuration (electronic supplementary material, figure S2) of this species [3,8]. We used the projections of the retinal areas with a higher density of photoreceptors (i.e. centres of acute vision) and with an overlap in visual resolution from the left and right eyes (i.e. binocular fields) to define an area around the head that would provide higher-quality visual information (figure 1c), compared with the projections of retinal areas with a lower density of photoreceptors (i.e. retinal periphery; electronic supplementary material, figure S2).

We constructed two robots from the skin of deceased starlings (one of each sex; electronic supplementary material). The robots had servos that generated movements mimicking three behaviours: head-down pecking, head-up scanning (through head movements) and rotational body movements (electronic supplementary material).

Given that the avian visual system configuration differs from humans, and that starling eyes do not have salient features (e.g. white sclera), we did not use eye movement cues to manipulate
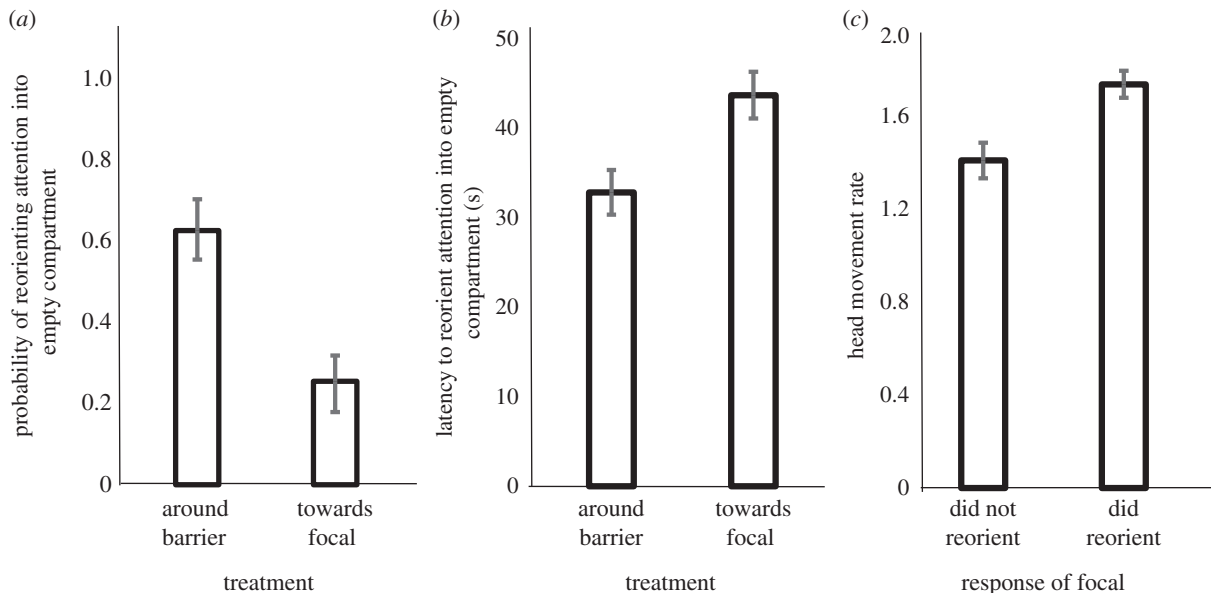
Figure 2. Probability of (*a*) and latency for (*b*) birds to reorient their attention through the window in the 'around barrier' and 'towards focal' treatments. (*c*) Head movement rate (events per second) of birds that did and did not reorient their attention into the empty compartment in the around barrier treatment. All error bars represent the standard error.

the visual attention of the robot. Instead, we used a combination of head and body orientation cues that mimicked the natural patterns of starlings (electronic supplementary material). A fixation cue consisted of the robot orienting its body in the direction of gaze and then moving its head sideways within a given range of angles (up to 90° left or right of the resting position of the beak) for two reasons. First, starlings generally keep their head relatively aligned with their body (electronic supplementary material). Second, given the large amplitude of head movements in starlings, and their relatively wide visual fields, manipulating both the head and body orientation simultaneously reduced the overlap in visual attention cues between treatments (electronic supplementary material).

We food-deprived the animals and allowed them to acclimate to the experimental arena for at least 2 min, while the robot was oriented towards the barrier (i.e. the sagittal axis of the robot was parallel to the barrier), scanning and pecking. Afterwards, we oriented the robot towards the focal compartment to get the focal attention through changes in the robot body and head orientation. We used a repeated measures design, exposing the focal to one of two treatments in each trial: (i) robot head and body remained oriented towards the focal compartment while scanning (towards focal treatment) or (ii) robot oriented towards the empty compartment around the barrier while scanning (around barrier treatment). Each bird was exposed randomly twice to each treatment on different days (i.e. only one treatment exposure per day). We used 23 starlings (12 males and 11 females).

We assessed whether the focal responded to the orientation behaviour of the robot when the latter looked into the empty compartment using the sensory criteria explained above. We estimated the probabilities of the focal reorienting its attention to the empty compartment using a generalized linear mixed model with a logit link function and binomial error distribution, with one independent factor (treatment) and subject incorporated into the model using a random statement and an autoregressive covariance structure (SAS v. 9.3, proc Mixed). Second, we recorded the latency for the focal to reorient its attention to either window facing the empty compartment (figure 1*b*). Birds that did not reorient their attention to the window were assigned a capped value of 51 s (i.e. overall length of the treatment) following Carter *et al.* [7]. The duration of the treatment was designed to give the live bird time to respond to the robot behaviour, which was originally 50 s; however, the script for the robot actually took 51 s to run on the computer. To analyse the latency data, we used a Freidman

two-way analysis of variance (Mantel–Haenszel method), with subject as our row factor and treatment as our column factor (SAS v. 9.3, proc Freq). In species with laterally placed eyes, the head movement rate (number of changes in head position per unit time) is a proxy of the degree of movement of the centres of acute vision [9]. We measured head movement rates of focals (electronic supplementary material) to assess their response using the same sensory modality that we manipulated in the robot behaviour (i.e. visual attention). Some bird species seem to fixate (i.e. focus visual attention on a single object) by exposing the right and left retinas alternately to an object [4]. Therefore, fixation on a given object (e.g. robot) may lead to an increase in head movement rates. We analysed head movement rates with general linear mixed models (SAS v. 9.3, proc Mixed) repeated on subject using an autoregressive covariance structure.

3. Results

The probability that the focal reoriented its attention to the window was significantly higher when the robot was looking around the barrier compared with when it was looking towards the focal ($\chi_1^2 = 11.49$, $p < 0.01$; figure 2*a*; electronic supplementary material, video S1). Additionally, focals reoriented their attention to the window significantly sooner when the robot was looking around the barrier compared with when it was looking towards the focal compartment, after adjusting for subject identity ($RR_{MH} = 8.65$, $p = 0.003$, $n = 83$; figure 2*b*).

The orientation behaviour of the robot (around barrier, towards focal) did not significantly affect head movement rates (movements per second, least square means ± s.e.) of focals that reoriented their attention ($F_{1,8} = 3.37$, $p = 0.104$, towards focal: 1.73 ± 0.08, around barrier: 2.03 ± 0.13) or that did not reorient their attention ($F_{1,10} = 0.08$, $p = 0.789$, towards focal: 1.42 ± 0.99, around barrier: 1.39 ± 0.07) to the empty compartment window. However, in the around barrier treatment, focals that eventually oriented their attention to the window had a significantly higher head movement rate before they reoriented than those that did not reorient their attention ($F_{1,8} = 11.65$, $p = 0.009$, figure 2*c*).

We also considered *post hoc* the possibility that the focals were *reflexively co-orienting* [10] (electronic supplementary material) their heads and bodies with that of the robot. However, we did not find support for this interpretation of our results (electronic supplementary material).

4. Discussion

To our knowledge, this is the first report of a non-mammal reorienting its attention geometrically in response to the orientation behaviour of *conspecifics* in a species with laterally placed eyes. This suggests that starlings recognize the location of conspecific attention. All species that have exhibited the ability to follow the attention of others geometrically when tested also showed this ability when attention was directed into distant space as well (e.g. [1,2,11,12]), but not necessarily the converse [1,2]. We cannot make conclusions about the sensory cues live birds used. One possibility is that starlings may have followed the gaze of conspecifics; however, they could also have reoriented their attention to changes in the robot's auditory or olfactory attention.

Starlings are a highly gregarious species that allocate a lot of time to monitoring conspecifics [13], even at the expense of losing foraging opportunities [14]. Starlings use social information to improve decisions about patch quality [6] and detecting predators [15]. We propose that recognizing the location of attention geometrically in starlings may provide information about the spatial location of events of interest. For instance, if the attention of an individual that has detected a predator draws the attention of other conspecifics to the predator, more individuals will have social information about the direction of predator approach allowing non-detectors to flush in the direction that minimizes the chances of mortality.

Additionally, responding to the orientation behaviour of conspecifics may accelerate the transfer of social information in flocks; for instance, following the attention of an individual could also draw the attention of more and more individuals to a specific location in the environment, leading to a quicker and more accurate response.

We also found evidence that responding to the orientation behaviour of conspecifics was associated with an increase in head movement rate. Individuals may have increased visual information sampling from the robot (presumably about its attention) before reorienting their own attention. Starling right and left retinas differ in the relative densities of photoreceptors [16], which influences the ability of each eye to discriminate different visual patterns [17]. This asymmetry may account for the increased head movement rate if starlings were trying to quickly obtain different types of information from the robot. This active information sampling may influence the chances of following somebody's attention. Dogs, for instance, appear to gather information about the attentional state of humans: looking directly to the dog increases its chances of gaze following [18].

Recognizing the location of another's attention could be a mechanism to facilitate the spatial coordination of social behaviour. Our study provides some methodological procedures (e.g. robotic birds, response criteria based on visual system configuration) to study shared attention in animals with sensory systems different from those of humans. Future studies should focus on the specific cues involved in shared attention by considering the configuration of different sensory dimensions and developing multimodal manipulations.

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