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Social birds copy each other's lateral scans while monitoring group mates with low-acuity vision

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Copying others can be used to enhance foraging and mating opportunities, but can be costly due to the need to monitor the actions of others, which can take time away from foraging and antipredator vigilance. However, little is known about the way animals monitor conspecifics. We investigated the mechanism that European starlings, *Sturnus vulgaris*, use to visually monitor group mates in perching situations through two questions. First, do starlings copy the timing of each other's vigilance? Second, do they use their centres of acute vision to monitor group mates? We studied a component of vigilance that has received relatively little attention, lateral scans, which consist of changes in the orientation of the head (i.e. gaze shifting) while in a head-up position. We found that starlings copied the timing of their neighbour's scans, placing them closer together in time than expected by chance. This could enhance the speed of social information spread within a group compared to random timing of head movements. The strength of this copying effect varied with neighbour distance and the sex of the follower and leader, suggesting that starlings appear to be more motivated to copy some individuals over others. Additionally, instead of monitoring neighbours with their centres of acute vision (high-quality vision), starlings tended to use their retinal periphery (low-acuity vision), potentially reducing the costs of social monitoring. Copying the timing of lateral scans may have advantages for gathering social information (i.e. quick responses to movements of group mates in situations such as murmurations). However, it can also have costs in terms of delaying the detection of personal information by any group member (e.g. predator attack) due to longer gaps without changes in gaze orientation. Therefore, copying the timing of lateral scans may be restricted to specific contexts (e.g. low predation risk).

Copying consists of imitating the actions of others. Copying can facilitate many fitness-related activities, such as choosing a mate (Losey, Stanton, Telecky, Tyler, & Zoology 691 Graduate Seminar Class, 1986), exploiting novel resources (Boogert, Nightingale, Hoppitt, & Laland, 2014), promoting appropriate levels of vigilance (Lipetz & Bekoff, 1982) and generating collective behaviours (Hemelrijk, van Zuidam, & Hildenbrandt, 2015). Copying can take on many modalities. Animals can copy behaviours (i.e. song: Slater & Ince, 1979; motion patterns: Hemelrijk et al., 2015; feeding behaviours: Dindo, Stoinski, & Whiten, 2011), spatial locations (i.e. local enhancement: Poysa, 1992; joint attention: Emery, 2000), or the timing of activities (e.g. vigilance versus sleeping: Beauchamp, 2011). Ecologically, copying can promote the formation of localized culture, such as dialects in songbirds (Slater & Ince, 1979) or novel feeding behaviours in primates (Dindo et al., 2011). These localized changes in behaviour can eventually lead to niche separation and speciation (Freeberg, 2000).

One of the gaps in our understanding of copying behaviour is the underpinning mechanisms. Copying requires animals to first monitor the behaviour of group mates, which could be costly (i.e. diverting time from other activities such as foraging, antipredator vigilance, etc.; Ward, 1985). There may be mechanisms that facilitate monitoring and allow copying to be less costly. Moreover, there are different ways to copy, some of which may be more beneficial in some situations than in others. Behavioural ecologists have studied copying the timing of vigilance bouts (head-up orientation) in relation to foraging bouts (head-down orientation) (Bednekoff & Lima, 2005; Fernández-Juricic, Siller, & Kacelnik, 2004; Ge, Beauchamp, & Li, 2011; Podgórski et al., 2016). Two strategies have been proposed to copy the timing of vigilance bouts: coordination and synchronization (Ge et al., 2011; Pays, Jarman, Loisel, & Gerard, 2007; Ward, 1985). During coordination, an individual has its head down when its neighbour's head is up, and vice versa. The

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benefit of coordination is that at any point in time, at least one group member is likely to detect a predator when it appears, enhancing escape responses due to earlier detection (Beauchamp, 2015; Bednekoff & Lima, 1998). However, this is at the cost of having fewer individuals gathering information about a particular threat at the same time, which may reduce the accuracy of assessing the direction of a potential predator attack (Bednekoff & Lima, 1998; Ward, 1985). During synchronization, group mates are more likely to be scanning at the same time with their heads up compared to a random strategy (Ge et al., 2011; Lipetz & Bekoff, 1982; Pays et al., 2007). The benefit of synchronization is that group mates can gather information about threat simultaneously, thereby enhancing the accuracy of the direction of a potential predator attack, but at the cost of time intervals with no vigilance.

Although birds spend a lot of time on foraging substrates, perching also occupies a large proportion of many species' daily routines (Feare, 1984) and it is important for the spread of social information (i.e. acquiring novel foraging task solutions, Boogert et al., 2014). While perching, birds do not have to trade-off foraging with vigilance, as they are oriented with the head up and typically engaged in lateral scans (i.e. moving their heads from side to side, Jones, Krebs, & Whittingham, 2007). These lateral scans change the location of the birds' visual attention, allowing them to 'update' their view of the space around them (Land, 1999; Dawkins, 2002). Lateral scans are important for gathering personal information (i.e. information gathered directly from the environment, such as finding food patches or spotting a predator) and social information (i.e. information gathered from the behaviour of others, such as the presence of conspecifics on a food patch or another individual flushing in response to a threat). For example, when cowbirds experience higher predation risk, they increase their lateral scanning rate, increasing the chances of spotting a predator (Fernández-Juricic, Beauchamp, & Bastain, 2007). Additionally, lateral scans in starlings have been shown to aid in the gathering of information about where a group mate was looking (Butler & Fernández-Juricic, 2014).

Copying (or imitating) the timing of a neighbour's lateral scan could occur in two ways, both of which have important consequences for predator detection through social information, and consequently, collective detection. First, an individual can move its heads shortly after the head movement of a group mate (i.e. lateral scans from neighbours would occur closer in time), leading to social information being detected sooner by group members (i.e. shorter information flow times) compared to independent head movement timing. However, this copying strategy could also lead to longer gaps in time when no group members engage in lateral scans (i.e. gaze shifts), potentially delaying the detection of an approaching predator. Second, an individual can delay moving its head after the head movement of a group mate (i.e. lateral scans from neighbours would be more spaced in time), leading to social information being detected more slowly by group members (i.e. longer information flow times) compared to independent head movement timing. However, this would lead to shorter gaps in time when no group member engages in lateral scans (i.e. gaze shifts), potentially decreasing the time to detect an approaching predator. Additionally, copying the timing of lateral scans would allow for new individuals that have just joined the group to adjust their vigilance levels to those of other group members that have been in the same spot for longer and therefore have a more accurate assessment of risk.

The first goal of this study was to characterize the temporal patterns of lateral scans in perching European starlings, *Sturnus vulgaris*. We used European starlings because their visual system has been well characterized (Dolan & Fernández-Juricic, 2010; Martin, 1986; Tyrrell, Butler, & Fernández-Juricic, 2015). Additionally many studies have found that starlings use social monitoring (Butler & Fernández-Juricic, 2014; Fernández-Juricic et al., 2004; Templeton & Giraldeau, 1995; Vásquez & Kacelnik, 2000). We predicted that starlings would tend to copy the timing of their neighbour's lateral scans due to their tendency to copy and synchronize other behaviours (e.g. head-up versus head-down patterns, foraging effort; Fernández-Juricic et al., 2004). To test this prediction, we used pairs of starlings and designated one bird as the focal ('responder') and the other bird as the nonfocal neighbour ('initiator'). We used pairs of birds rather than larger group sizes because we were interested in the fundamental mechanisms of copying lateral scans and having larger groups would have added multiple sources of social information (e.g. several neighbours in different spatial positions moving their heads simultaneously), making measurements (and inferences) more challenging. We also examined whether copying is influenced by the sex composition of the group. Starlings are polygynous, with females forming groups of two to four individuals that mate exclusively with a single male and exclude other females from their group (Feare, 1984; Henry, Bourguet, Coulon, Aubry, & Hausberger, 2013). Males must compete with each other for access to these female groups (Feare, 1984). Additionally, under limited food resources, females show impaired auditory learning relative to males, and males show decreased flying abilities relative to females (Farrell, Morgan, & MacDougall-Shackleton, 2016; Verspoor, Love, Rowland, Chin, & Williams, 2007).

Our second goal was to investigate the role of the visual system (e.g. use of acute versus peripheral vision) in monitoring group mates. This is relevant in the context of copying because monitoring others is expected to be costly (Ward, 1985), but these costs have been proposed to be lower for some visual sensory configurations (e.g. wide visual fields; Fernández-Juricic et al., 2004). Starlings have laterally placed eyes, with one centre of acute vision (i.e. fovea) in each eye projecting laterally to two different points in space (Fig. 1a). In addition, their centres of acute vision do not project into the binocular field even when the eyes are converged (see Supplementary Fig. S1). The other areas of the retina (i.e. retinal periphery) provide relatively lower visual resolution, projecting into different parts of the visual field (binocular field, front and rear periphery; Fig. 1a). Finally, starlings have a region of the visual field, the blind area, with little or no visual input except when the eyes are diverged (Supplementary Fig. S1b). We addressed this second goal in multiple ways. First, we established the regions of the visual field (i.e. binocular, foveal, peripheral) that starlings use to monitor their neighbours at different neighbour distances. Based on Dawkins's (2002) findings in chickens, we predicted that starlings would use their binocular fields when they were close to conspecifics (Fig. 1a, dark grey region) but would use their foveae when farther away. Since the flow of social information degrades with distance (Fernández-Juricic & Kowalski, 2011), we predicted that birds would respond more slowly to conspecifics that were farther away. We also examined whether body orientation influences patterns of lateral scanning. We predicted that starlings would be quicker to respond to each other when their bodies were in parallel (i.e. bodies oriented in the same direction, Fig. 1b) than when they were antiparallel (i.e. bodies oriented in opposite directions, Fig. 1b) due to the spatial configuration of their visual system. Starlings have foveae that project slightly forward (about 60.5° caudally of the beak; Martin, 1986; Dolan & Fernández-Juricic, 2010), making the alignment of the centre of acute vision of the focal individual relative to the nonfocal individual easier when the two individuals are oriented in parallel as opposed to antiparallel. Finally, we examined whether the part of the visual field (i.e. binocular, foveal, etc.) used by the focal individual to monitor its neighbour would influence the focal's behavioural

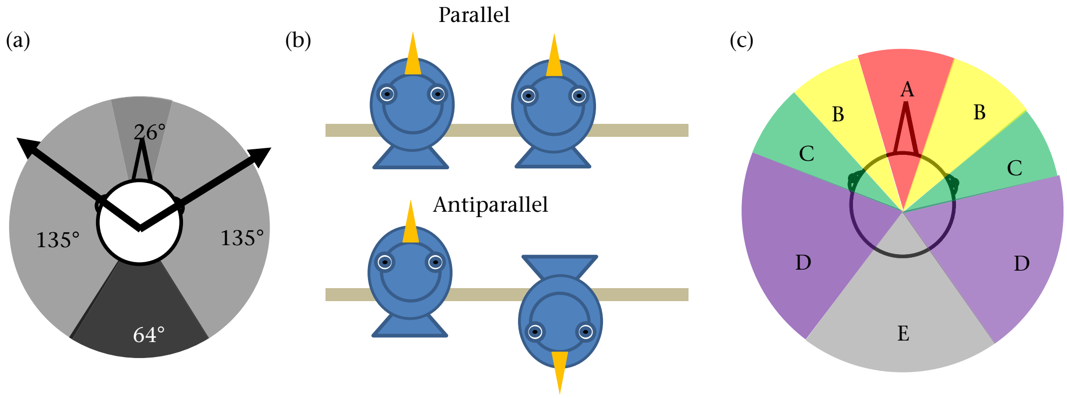

Figure 1. (a) Visual field of a European starling, *Sturnus vulgaris*. Light grey indicates where one eye can see, dark grey indicates where both eyes can see (i.e. the binocular field) and black indicates where neither eye can see (i.e. the blind area). Reproduced from Martin (1986). (b) Body orientations when birds are in parallel and antiparallel orientation. (c) Division of the visual field of European starlings based on Martin (1986) and Dolan and Fernández-Juricic (2010). We divided the visual field into five categories: (A) the resting binocular field; (B) front periphery, the region in front of the most converged position of the fovea and the binocular field; (C) foveal area, the sector between the most diverged and converged position of the fovea; (D) rear periphery, the sector behind the most diverged position of the fovea and the blind area; and (E) the blind area.

response using two measures: (1) latency to respond and (2) the magnitude of the focal's head movement. The latency to respond can influence the speed with which information flows, and the magnitude of a head movement can influence the saliency of cues available to conspecifics (i.e. large head movements may be more salient to neighbours).

METHODS

Housing and Capture

We conducted this experiment from November 2014 through to February 2015. We captured the birds in December 2013 using modified decoy traps in Hamilton County, Ohio, U.S.A. (39°16′60″N, 84°35′41″W) and transported them to the Ross Biological Reserve, Tippecanoe Country, Indiana, U.S.A. (40°25′0″N, 87°4′9″W). The state of Ohio does not require a permit to capture European starlings because starlings are an invasive species. There is also no required paperwork to transport European starlings from Ohio to Indiana according to the state and federal organizations (Ohio Department of Natural Resources: Wildlife; Indiana Department of Natural Resources: Fish and Wildlife; Unites States Department of Agriculture, APHIS, Wildlife Services). We housed birds in outdoor aviaries (2.5 × 2.5 × 3.5 m) in mixed-sex groups and provided food (cat food and game bird maintenance chow) and water ad libitum. Several days before the trials, we moved the birds to indoor enclosures in groups of two to four to habituate them to the experimental arena. The Purdue Institutional Animal Care and Use Committee (protocol 1306000876) approved all procedures for animal handling.

Experimental Arena and Procedures

The experimental arena consisted of a black wire enclosure, measuring approximately 1 m^3, with an ultraviolet-transmitting Plexiglas top (Loop Acrylics, Chicago, IL, U.S.A.). We placed the enclosure on top of a table covered in brown butcher paper and surrounded the table with black curtains to screen out visual noise and reduce the chances of the focal's head movements being due to external stimuli. We secured a wooden perch 20 cm from the bottom of the enclosure. The birds were able to move along this perch during the experiment. An overhead camera (JVC Everio Full HD) provided a view of the birds' heads in most occasions. However, there were several instances where the head of one bird was not visible because the animal was at the very edge of the perch, but this happened in less than 1% (85/9188) of the total head movements recorded, so we excluded these measurements from the analyses.

Based on which birds were present in the indoor housing facility, we arbitrarily chose pairs of individuals for the trials: focal and nonfocal (i.e. neighbour). We housed each pair in the same enclosure for at least 1 day before each trial to familiarize the birds with each other. We tested 23 starlings (13 females, 10 males) as focals. Each bird served as a focal three times, and also participated as a nonfocal in additional trials. Furthermore, some birds participated only as nonfocals. Each bird participated (as either focal or nonfocal) in a maximum of one trial per day, with at least 2 days between trials. The pairings resulted in 31 opposite-sex pairs, 15 female pairs and 23 male pairs. Birds concurrently participated in another behavioural experiment about visual fixation (where they were exposed to treatments individually), but never within 48 h of a trial in the present experiment. In one trial, the birds never perched together, so we reran that trial with the same focal but a different nonfocal on a different day.

We deprived the animals of food the evening before trials to standardize their physiological state. Immediately before the trial, we weighed both birds and marked the focal with a dot of nontoxic paint on the centre of its head. Marking birds with paint is common and does not seem to affect the bird's behaviour (Burt, 2002). The experimenter (either C.H. or S.R.B.) placed both birds in the experimental arena and then hid behind the black curtain that surrounded the experimental arena. Each trial lasted 5 min, after which the birds were returned to their housing enclosures.

Video Coding

We excluded data from the first minute of the trial as the experimenter had just left the arena. If the birds were calm (i.e. flew off their perch fewer than four times/minute), we coded the next 2 min segment of the video, and if not, we coded a 2 min segment later in the video. We included only portions of time when both birds were on the perch and when neither bird was preening.

We coded the trials to assess the focal's response to the head movements of the nonfocal using QuickTime v.7 (at 30 frames/s). We identified all of the head movements of the nonfocal that occurred when the focal's head was stationary rather than moving because visual input is constrained while the head is in motion (Burr, Morrone, & Ross, 1994; Land, 1999). To exclude the possibility that the head movements of the focal were due to individual vigilance patterns (i.e. independent of the nonfocal), we assessed the latency for the focal to turn its head towards or away from the nonfocal, measured from random points in time as opposed to relative to the nonfocal head movements, but still in the presence of the nonfocal. We picked 100 random frames per trial and recorded the latency for the focal to move its head after these random frames.

We made the following three predictions. (1) If head movements are more synchronous than expected by chance, then the focal's latency to move its head after the nonfocal has moved its head should be significantly shorter than the focal's latency to move its head after a random frame. (2) If head movements are less synchronous than expected by chance, then the focal's latency to move its head after the nonfocal has moved its head should be significantly greater than after a random frame. (3) If the timing of the focal's head movements is independent of the nonfocal's head movements (i.e. no copying), then the focal's latency to move its head after the nonfocal has moved its head should not differ significantly from the latency for the focal to move its head after a random frame.

We specifically chose our sampling method to assign in advance one bird as the nonfocal (initiator) and one bird as the focal (responder) for two reasons. First, this sampling approach allowed us to statistically detect the difference between the head movements being closer together or further apart in time. Had we picked an initiator and a responder post hoc, we would not have been able to statistically detect the difference between the timing of the focal and nonfocal head movements. Second, while birds move their heads, visual input is limited (Burr et al., 1994; Land, 1999); thus, we chose to sample only instances when the focal's head was not in motion as the nonfocal initiated a head movement because the focal might not have been able to detect it visually. Our sampling approach could double count head movements (i.e. having one head movement of the focal counted as a response to two different head movements of the nonfocal, or in response to two random frames), leading to longer latencies in response to the first nonfocal head movement. To minimize this bias, we assumed that the response of the focal was to the head movement of the nonfocal immediately preceding, and not to any other head movement that occurred before this. Thus, we conditioned the data set to include only pairs of head movements where the focal was the next bird to move its head after the nonfocal. For instance, if the nonfocal had made two head movements in a row before the focal moved its head, we only included the nonfocal's second head movement. Similarly, we excluded random frames that were not followed by a focal head movement before the next random frame.

One observer (C.H.) identified any head movements that were detectable by watching the videos frame by frame, where the bird's head was in a different position in two consecutive frames. C.H. excluded head movements that were up or down (not identifiable as towards or away from the other bird), which happened less than 1% of the time (65/9188 head movements). C.H. was 95% consistent with herself in terms of identifying these head movements. We included all head movements that followed the above criteria, even very small ones, meaning that we did not have a ‘cutoff’ amplitude. C.H. also recorded the distance between the birds (in cm), and whether their bodies were oriented in parallel (i.e. in the same direction) or antiparallel (in opposite directions) (Fig. 1b) relative to each other. Five people coded other aspects of the videos. After S.R.B. engaged in self-training, and once she and the other four individuals were 95% consistent with each other in identifying the end of head movements within two frames (at 30 frames/s) of each other, they identified the end of all the head movements.

We also examined how starlings used their visual system in these interactions. S.R.B. measured the angle of the focal's head relative to the perch at the start and end of each head movement to the nearest degree, using a clear plastic protractor with a string attached. S.R.B. was 95% consistent within 2° after self-training. We then projected the location of the nonfocal into the focal's visual field. All these calculations were based on published accounts of the European starling retinal configuration (Dolan & Fernández-Juricic, 2010) and visual fields (Martin, 1986).

Animals that can move their eyes, such as European starlings (Martin, 1986; Tyrrell et al., 2015), have a dynamic visual field: the size of the binocular field, the lateral field and the blind area changes depending on whether the eyes are at rest or are converged or diverged (Fig. S1). We used this sensory information to divide the focal visual field into five categories, while assuming that the eyes were at rest (Fig. 1c): resting binocular field, resting blind area, foveal area, front periphery and rear periphery. We assigned the resting binocular and resting blind area based on the measurements of the binocular field and blind areas with the eyes at rest (Fig. 1a). This means that in the area labelled ‘resting blind area’, starlings can actually gather some visual information when their eyes are diverged (Fig. S1). Although we made the assumption that the eyes were at rest, the fovea is a small spot on the retina and using just that projection would correspond to a point rather than a region in the visual field. However, starlings move their eyes (and therefore their fovea) often (Tyrrell et al., 2015), so we defined the foveal area as the sector of the visual field subtended by the fovea between the maximally converged and maximally diverged positions of the eyes (Fig. S1). Finally, we assigned the regions in front of and behind the foveal area as the front and rear periphery, respectively. We also used these angles to calculate the magnitude of each of the focal's head movements by subtracting the final position from the initial angle for each head movement.

Finally, monitoring of another individual can provide information about the identity (Henry et al., 2013) and sex (Pyle, 1997) of that individual. Therefore, we also considered in our statistical analyses the sex of the focal and the nonfocal. However, we did not have any a priori hypothesis about how males and females would respond to group mates.

Statistical Analyses

We ran all analyses with SAS v.9.3 (SAS Institute, Cary, NC, U.S.A.). We used a generalized linear mixed model whenever the response variable was categorical, frequency or latency, which would not be expected to follow a normal distribution. We chose link functions based on either predicted distributions when applicable, or whichever distribution or matrix fit best (using −2loglikelihood ratio). For the analysis involving magnitude, we used a general linear mixed model. All analyses used repeated measures with focal as the subject variable to avoid pseudoreplication. All analyses used the between−within method to calculate the degrees of freedom. We used an alpha value of 0.05 to determine statistical significance.

To assess whether the timing of scans followed either of the two copying patterns (see Introduction) or was independent, we used a generalized linear mixed model, with a log link function and a Poisson error distribution. We used latency of the focal to turn its head after the nonfocal head movement as the dependent factor, or a random frame as described above to generate the latency that would be expected if timing of head movements is independent. For our independent factors, we used the event (nonfocal head movement or random frame) that preceded the focals head movement. Our other independent covariates were: sex of the focal (male/female); sex of nonfocal (male/female); the interaction between nonfocal and focal sex (male focal with male nonfocal, female focal with male nonfocal, male focal with female nonfocal, and female focal with female nonfocal); the body orientation of the birds (parallel/ antiparallel); and the distance between the birds (continuous, in cm). We used a distance-squared term to check for linearity of the nonfocal distance. If starlings were copying the timing of each other's head movements, we would expect a significant main effect of the event preceding the focal head movement (i.e. latency would be significantly shorter or longer after a nonfocal head movement compared to a random frame).

We also assessed the relationships between the different independent factors because neighbour distance, body orientation and sex could be related to each other directly or indirectly. We examined pairs of variables that could have plausible associations between each other (i.e. neighbour distance on body orientation, body orientation on neighbour distance, sex on body orientation, sex on neighbour distance) in their own mixed model with repeated measures to control for multiple measurements on each focal. We did not examine relationships that had no plausible explanation (i.e. body orientation cannot affect sex). We used a generalized linear mixed model when the dependent variable was latency or categorical, and a general linear mixed model when the dependent variable was continuous. We then calculated the effect size of each pair of variables examined. Additionally, for all independent factors, we estimated the effect size on latency (dependent variable) using Cohen's *d* with pooled variances both by themselves and in their own model (see Results, Fig. 2). For all other analyses, we calculated the effect size of each independent factor within the model while controlling for all other independent factors (see Results, Tables 1, 2). When the independent factor had more than two levels, we determined the effect size by averaging the absolute value of all calculated pairwise effect sizes. To interpret the results, we followed the conventional classifications of effect sizes: negligible: <0.2; small: between ≥0.2 and <0.5; medium: between ≥0.5 and <0.8; large: >0.8.

We also plotted the cumulative distributions of focal latency for head movements following the nonfocal and random frames and performed a two-sample Kolmogorov–Smirnov test to establish whether the pattern of response to the nonfocal head movements (copying, random) varied with time since the generalized linear mixed model only provided insights to what happens on average. For the Kolmogorov–Smirnov test, we used a bin width of 100 ms, allowing us to determine the length of time over which copying differed from chance.

We examined whether the behavioural response of the focal (latency to respond and the magnitude of the head movement) varied with the region of the visual field (right before the beginning of its head movement) used to monitor the nonfocal. To analyse latency, we used a generalized linear mixed model with a Poisson error distribution, where the region of the visual field was the independent factor. To analyse the magnitude of the head movement, we used a general linear mixed model with a normal distribution, with the region of the visual field included as the independent factor. For both of these analyses, we controlled statistically for the distance between the birds and the sex of both birds and the interaction between the sex of the focal and the nonfocal.

We also examined whether the region of the visual field that starlings used to orient towards the nonfocal (right after the end of a head movement) varied with distance. We did this in three steps to ensure that we used appropriate statistical methods but also could interpret our results in a meaningful way. We first tested whether the region of the visual field used to orient towards the nonfocal varied with distance. We did this by using distance as a continuous independent factor in a generalized linear mixed model with region of visual field (5 categories) as the dependent variable and a multinomial error distribution. This first step (treating distance as continuous) was necessary to ensure that our categorization was not arbitrary. Once we established that distance influenced the region of the visual field used ($F_{1,4954} = 6.19$, $P = 0.013$), we divided distance into three categories (close, intermediate, far) such that each distance had equal sample sizes. We then ran a generalized linear mixed model with a multinomial error distribution using region of visual field (5 categories, see Results, Fig. 4b) as the dependent variable and distance (categorical, 3 levels) as the independent factor, again including focal sex, nonfocal sex and the interaction of these two factors as covariates. We ran pairwise contrasts to determine specifically which distance categories differed in the distribution of the region of the visual field that was oriented towards the nonfocal. To interpret the direction of these relationships, we plotted the raw means of the proportion of scans that ended in each visual field sector.

We also asked whether the latency for the focal to respond was correlated with the magnitude of its head movement. We predicted that short latencies would be correlated with larger magnitudes of head movements because we assumed that both measures result from the same motivational level.

RESULTS

Timing of Head Movements

The latency for the focal to make a head movement after the nonfocal's head movement was significantly influenced by the event preceding the focal head movement (nonfocal head movement or random frame) (Table 1, Fig. 2a). More specifically, the average latency was significantly shorter than that predicted by chance (i.e. random) (Table 1, Fig. 2a), suggesting that the focal and nonfocal head movements were more closely spaced in time. The sex of the nonfocal and the focal significantly influenced the strength of this copying effect, although their interaction was not significant (Table 1). Female focals responded more quickly to the nonfocal, regardless of the nonfocal's sex (Fig. 2c). Focals of either sex responded more quickly to male nonfocals (Fig. 2d). Body orientation, sex of the focal and sex of the nonfocal all had large effect sizes (Table 1). The interaction between the sex of the focal and the nonfocal had a negligible effect size (Table 1).

The latency between a nonfocal's head movement and a focal's head movement was significantly affected by distance, in a nonlinear way (linear term: coefficient = 0.01043; squared term: coefficient = −0.00027; Table 1), resulting in a unimodal, parabolic distribution of latency that peaked (i.e. longest latency, weakest copying) at 19 cm and was lower (i.e. shorter latency, more pronounced copying) on either side of this peak (Fig. 2e). Additionally, body orientation influenced the latency for the focal to respond to the nonfocal (Table 1), with individuals responding sooner when they were oriented in antiparallel positions (i.e. with their bodies oriented in opposite directions relative to each other) compared to parallel (latency least square means ± SE: antiparallel = 227 ± 4 ms; parallel = 250 ± 3 ms). Distance and distance squared had negligible effect sizes while body orientation had a large effect size (Table 1).

We also found that the copying effect primarily took place over the first 100–500 ms after the nonfocal moved its head (Kolmogorov–Smirnov test: critical value $D^{*}_{23,23} = 0.087$; Fig. 2f shows these critical values as vertical dotted lines). Thus, when an individual copied the timing of the nonfocal's head movement, it usually did so within half a second.

We found that sex had large effect sizes on both the distance between the focal and the nonfocal and their body orientations (Fig. 3). On average, female–female pairs were farthest from each

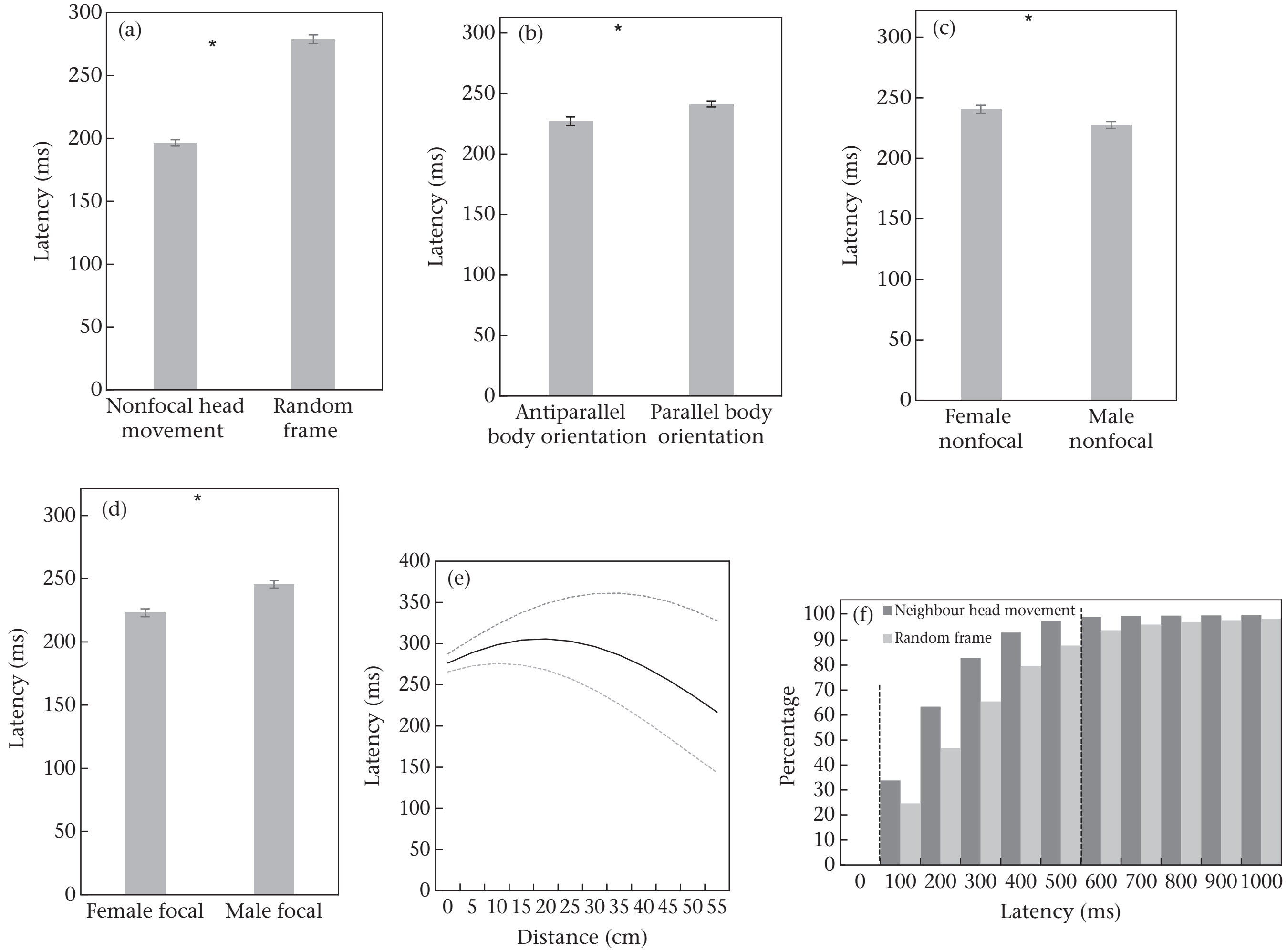

Figure 2. The focal's latency to respond relative to (a) an event (nonfocal's head movement versus a random video frame), (b) the body orientation of the nonfocal (antiparallel versus parallel), (c) the sex of the nonfocal and (d) the sex of the focal. (e) Relation between neighbour distance and the focal's latency to respond. The grand mean of latency over distance was plotted by running the model without any random factors. Grey lines represent the standard error. (f) Cumulative distribution of head movements over latency. Statistically significant copying occurred when latency was between 100 and 500 ms, as indicated by the vertical dashed lines.

Table 1
Effects of independent factors on latency for focal to move its head

	F	*df*	*P*	Cohen's *d*
Event[a]	425.45	1, 22	**<0.0001**	8.80
Distance	9.79	1, 9159	**0.0018**	0.07
Distance∗distance	17.82	1, 9158	**<0.0001**	0.09
Body orientation	10.95	1, 18	**0.0039**	1.56
Sex of focal	29.66	1, 21	**<0.0001**	2.38
Sex of nonfocal	9.53	1, 16	**0.0071**	1.55
Sex of focal∗sex of nonfocal	1.35	1, 16	0.2615	0.58
Category of visual field[b]	5.85	4, 87	**0.0003**	0.37[c]
Distance	3.37	1, 4947	0.0663	0.05
Distance∗distance	7.28	1, 4948	**0.007**	0.08
Sex of focal	3.8	1, 16	0.0692	0.80
Sex of nonfocal	2.38	1, 21	0.1377	0.40
Sex of focal∗sex of nonfocal	0.84	1, 16	0.3727	0.46

Statistically significant effects are shown in bold.

[a] Analyses involving event, controlling for distance, distance squared, body orientation and the sex of the focal and nonfocal.

[b] Analyses involving category of visual field used to monitor neighbour, controlling for distance, distance squared, body orientation and the sex of the focal and nonfocal.

[c] Effect sizes for categorical variables with more than two levels were calculated using the averaged absolute values of the effect sizes for all pairwise comparisons between levels.

Table 2
Effects of independent factors on the category of the visual field that the focal bird used to orient towards the nonfocal bird after the nonfocal's head movement

	F	*df*	*P*	Cohen's *d*
Distance	9.92	1, 4951	**0.0016**	0.09
Distance∗distance	6.25	1, 4951	**0.0124**	0.07
Sex of focal	0.13	1, 18	0.7236	0.10
Sex of nonfocal	9.39	1, 16	**0.0074**	0.11
Sex of focal∗sex of nonfocal	8.13	1, 16	**0.0115**	1.43

Statistically significant effects are shown in bold.

other (mean ± SE = 26 ± 1.5 cm) and in parallel most often (75 ± 1%) compared to other sex compositions, while male–male pairs were closest to each other (19 ± 1.5 cm) but in parallel least often (63 ± 0.9%) relative to other sex compositions, and mixed-sex pairs fell in between single sex pairs with respect to these two factors (distance: 21 ± 1.5 cm; percentage of scans in parallel: 67 ± 0.1%). The effect size of distance on body orientation was negligible, but there was a strong effect size of body orientation on distance, with birds that stood in parallel standing closer together (21 ± 1.5 cm) than birds in antiparallel (23 ± 1.5 cm) (Fig. 3).

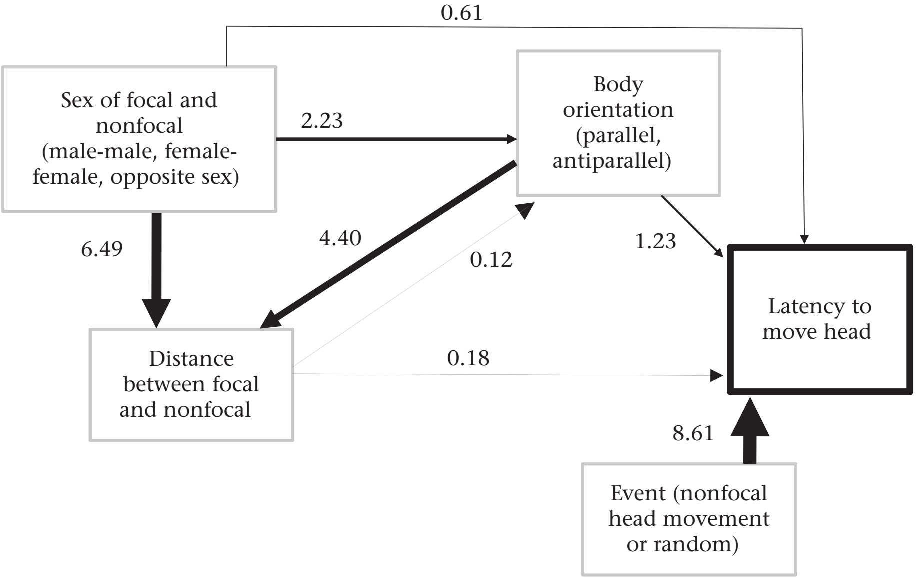

Figure 3. Effect sizes of sex, neighbour distance, event (neighbour's head movement or random frame; see text for details) and body orientation on each other. Effect sizes were calculated using Cohen's *d*. The effect size for distance on latency and distance on body orientation is an average of the effect sizes from the linear and nonlinear terms. Effect sizes were calculated using general (for continuous, normal dependent variables) or generalized (for categorical or non-normal dependent variables) with only one independent and one dependent variable. The effect sizes presented here differ from those presented in Tables 1–3 because those in Tables 1–3 were calculated with the full models controlling for the other independent factors.

Region of Visual Field Used to Monitor the Group Mate

Figure 4a shows the frequency distributions of lateral scans associated with different regions of the visual field across different distances, with the grey dotted lines representing the expected frequency distributions if the focal were to use its visual field based on the relative sizes of its different components. We found that the frequency distributions of lateral scans were significantly influenced by nonfocal distance (i.e. close, intermediate, far) ($F_{2,36} = 9.00$, $P = 0.0007$; Fig. 4a), suggesting that the region of the visual field that focals tended to use to orient towards the nonfocal varied with distance. More specifically, we found differences between close and far ($F_{1,36} = 16.62$, $P = 0.0002$), and close and intermediate ($F_{1,36} = 7.86$, $P = 0.0081$), but not between intermediate and far distances ($F_{1,36} = 1.75$, $P = 0.194$). The trends suggest that starlings used the front portion (binocular field and front periphery) of their visual field to orient towards nonfocals at closer distances, but they used the back portion (blind area and rear periphery) more often when nonfocals were farther away (Fig. 4a).

The region of the visual field that the focal used to orient towards the nonfocal was influenced significantly by the nonfocal's sex, the interaction between the sex of the focal and the nonfocal, but not by the sex of the focal (Table 2). The sex of the nonfocal had a negligible effect size, but the interaction between the sex of the focal and the sex of the nonfocal had a large effect size. To interpret these results, we categorized the data by sex composition of the pair (male–male, female–female, mixed-sex pair). Figure 4b shows the frequency distributions of lateral scans associated with different regions of the visual field considering the sex composition of the pair, with the grey dotted lines representing the expected frequency distributions if the focal were to use its visual field based on the relative sizes of its different components. We found that the distribution of the regions of visual field was significantly different between all pairwise comparisons (female–female versus male–male pairs: $t_{16} = 16.05$, $P < 0.0001$; female–female versus mixed-sex pairs: $t_{16} = 8.15$, $P < 0.0001$; male–male versus mixed-sex pairs: $t_{16} = 9.33$, $P < 0.0001$). The focal tended to orient its binocular field towards the nonfocal more in female–female pairs than in male–male or mixed-sex pairs (Fig. 4b). However, the focal tended to orient its resting blind area towards the nonfocal less in female–female pairs than in male–male pairs, but more than in mixed-sex pairs (Fig. 4b). Overall, in female–female pairs, focals more often oriented the front of their visual field towards the nonfocal, while in male–male pairs, focals more often oriented the back of their head towards the nonfocal, and in mixed-sex pairs, the focal's orientation tended to be somewhere in between.

We found that the behavioural response of the focal differed in latency and magnitude depending on the sector of visual field that the focal had used to orient towards the nonfocal, after controlling for the effects of nonfocal distance and sex (Tables 1, 3, Fig. 4c,d). Latency was the shortest (i.e. fastest) when the blind area was directed towards the nonfocal (Fig. 4c). Latency was also shorter for the front periphery than for the rear periphery (Fig. 4c). Finally, when focals directed their resting blind area towards the nonfocals, they made a greater head movement than when any other region of the visual field was oriented towards the nonfocal (Table 3, Fig. 4d). The category of visual field had a medium effect size on both latency and magnitude (Table 1, 3).

We found that magnitude was negatively correlated with latency, and that this trend was influenced by nonfocal distance, distance squared and nonfocal sex, but not the focal sex or the interaction between the nonfocal and focal sex (Table 3). Focals (regardless of sex) made greater head movements in response to males than in response to females. Birds' distance was associated with magnitude in a nonlinear way (Table 3), peaking (i.e. highest magnitude) around 34 cm and being lower when birds were either closer or farther away. The effect size of the nonfocal sex was large, but the effect sizes of distance and distance squared were negligible.

DISCUSSION

Group mates in social foraging aggregations have been assumed not to monitor the vigilance of neighbours because it would take

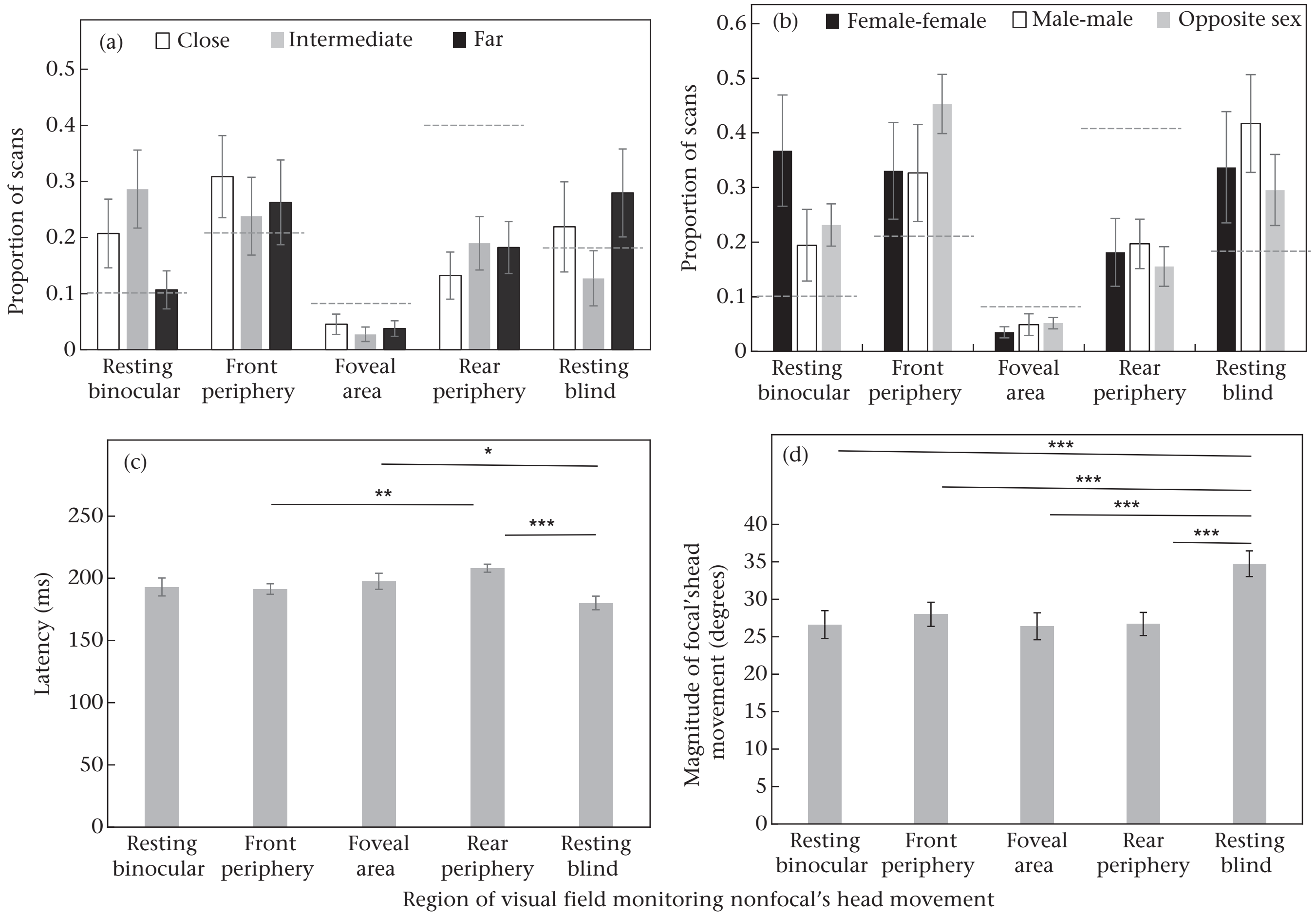

Figure 4. (a) Proportion of scans in which the focal individual oriented towards the nonfocal individual at close, intermediate and far neighbour distances. (b) Proportion of scans in which the focal individual oriented towards the nonfocal individual in male–male, female–female and male–female pairs. In (a) and (b), the grey dotted lines represent the expected frequency distribution of scans based on the relative size of each component of the focal's visual field. (c) Focal individuals' latency to respond to the nonfocal's head movement based on the region of the visual field used to monitor the nonfocal's head movement. (d) Magnitude of the focal's head movement based on the region of the visual field used to monitor the nonfocal's head movement.

time away from being vigilant or foraging (Beauchamp, 2002; Ward, 1985). However, more recent evidence suggests that birds do monitor each other, particularly starlings (Fernández-Juricic et al., 2005; Templeton & Giraldeau, 1996), even at the expense of decreased food intake (Vásquez & Kacelnik, 2000). Our study is the first to show evidence for a potential mechanism to monitor neighbours' behaviour in a perching context through lateral scans. More specifically, we found that starlings copied the timing of each other's lateral scans by moving their heads (i.e. shifting gaze) shortly after their group mates moved theirs. The strength of this copying effect was most pronounced at close and far neighbour distances, when the responder was a female, and when the initiator was a male. Irrespective of neighbour distance, starlings tended to monitor their group mates with low-acuity vision rather than high-acuity vision.

Table 3
Effects of independent factors on magnitude of focal's head movement

	F	*df*	*P*	Cohen's *d*
Category of visual field[a]	16.66	4,87	**<0.0001**	0.63[c]
Distance	14.89	1,4948	**0.0001**	0.11
Sex of focal	0.1	1,21	0.7496	0.38
Sex of nonfocal	7.79	1,16	**0.0131**	0.24
Sex of focal∗sex of nonfocal	4.83	1,16	**0.043**	1.10
Latency[b]	30.42	1,4950	**<0.0001**	0.16
Distance	23.28	1,4951	**<0.0001**	0.14
Distance∗distance	13.37	1,4952	**0.0003**	0.10
Sex of focal	0.11	1,21	0.7414	0.05
Sex of nonfocal	19.33	1,16	**0.0005**	1.81
Sex of focal∗sex of nonfocal	0.23	1,16	0.6411	0.24

Statistically significant effects are shown in bold.

[a] Analyses involving category of the visual field used, controlling for distance and the sex of the focal and nonfocal.

[b] Analyses involving latency to respond, controlling for distance, distance squared and the sex of the focal and nonfocal.

[c] Effect sizes for categorical variables with more than two levels were calculated using the averaged absolute values of the effect sizes for all pairwise comparisons between levels .

Starlings have previously been found to synchronize their vigilance bouts (i.e. head-up and head-down sequences) with neighbours (Fernández-Juricic & Kacelnik, 2004) and follow each other's gaze (Butler & Fernández-Juricic, 2014). The lateral scan copying strategy we found in the present study could accelerate the flow of social information: an individual that copies the timing of its group mates' gaze shifts would be quicker to detect changes in their head movements than an individual that initiates its lateral scans independently of its group mates. This could explain why starlings are able to respond so quickly to their neighbour's movements in flocks (Hemelrijk et al., 2015), and potentially in murmurations. Since the timing of head movements is associated with perceived risk (Fernández-Juricic, Beauchamp, Treminio, & Hoover, 2011), copying the lateral scans of group mates could help maintain a similar baseline scanning level across the group. Yet this type of copying behaviour would lead to longer gaps where no changes in gaze orientation occur, which could delay the detection of personal information (e.g. an approaching predator) by any group member. It is possible, however, that our results were influenced by the relatively low predation risk conditions of our experimental set-up, so future studies should test this type of lateral scan copying behaviour under situations with different levels of perceived risk.

Neighbour distance significantly influenced the strength of lateral scan copying in a nonlinear (inverse-U) fashion. Actually, neighbour distance has previously been proposed to affect the flow of social information in groups nonlinearly (Proctor, Broom, & Ruxton, 2003). Empirical studies support this prediction in contexts of vigilance (Rolando, Caldoni, Sanctis, & Laiolo, 2001) and neighbour detection (Fernández-Juricic & Kowalski, 2011). However, in these studies, the response appeared to level off with distance, whereas we found an inverted U-shape relationship: starlings copied lateral scanning when neighbours were either close or far away. Visual resolution decreases with distance, which can decrease the probability of detecting social cues (Fernández-Juricic & Kowalski, 2011). However, after a certain distance, individuals may compensate for the lower resolution by responding more quickly to any group mate movement. The implication is that individuals may weigh the lateral scans from nearby neighbours differently depending on their absolute neighbour distance by using different parts of their visual field. Starlings tended to use their binocular fields more when looking at their neighbour at close and intermediate distances compared to far distances, similar to what Dawkins (2002) found in chickens.

Starlings appeared to be more motivated to copy some individuals over others. First, females copied their neighbour (whether male or female) more quickly than males, and both sexes copied males more quickly. This could be due to the dominance of males over females in the starling mating system (i.e. polygynous; Feare, 1984). This relationship between dominance and social information use is also found in dwarf mongooses, *Helogale parvula*: they use social information about predators more when the source is a dominant individual compared to a subordinate individual (Kern, Sumner, & Radford, 2016). Second, the magnitude of the focal's head movement was negatively correlated with latency to respond: individuals that responded more quickly also tended to show greater head movements, whereas those that took longer to respond also tended to show smaller head movements. Large head movements occurred more often in response to a male neighbour than to a female neighbour. Third, females tended to orient the front of their head towards their neighbour more when paired with another female, likely because coloration of the beak can provide information about sex, breeding status and overall health (Navarro, Pérez-Contreras, Avilés, Mcgraw, & Soler, 2010; Pyle, 1997). In contrast, males tended to orient the rear of their heads towards their male neighbours, possibly to avoid costly aggressive interactions associated with the beak (Nephew, Aaron, & Romero, 2005).

Starlings have a relatively wide visual coverage, being able to see approximately 296° around their head (Martin, 1986). Within this large field of view, there are small areas with high (i.e. fovea) and low visual acuity (i.e. retinal periphery). We found that instead of monitoring neighbours with the centre of acute vision, starlings use retinal areas with lower visual resolution (i.e. retinal periphery). We speculate that although starlings may monitor group mates with their visual periphery, they may only allocate a small amount of attention to them, leading to a low-cost strategy (i.e. not taking up the neural resources devoted to the centre of acute vision). This would be enough to detect pronounced changes in the neighbours' behaviour that do not require high visual resolution (i.e. a neighbour changing its lateral scanning strategy abruptly), but possibly not enough to pick up on more subtle changes. One of the sensory drawbacks of using the visual periphery is the increase in the degree of uncertainty (entropy) of a cue (Dall, Giraldeau, Olsson, Mcnamara, & Stephens, 2005). However, animals could compensate behaviourally for this sensory constraint. We found that starlings responded more quickly and with larger amplitudes of head movements when the neighbour was aligned with their resting blind areas (i.e. very edge of the retina with extremely low acuity or no vision at all), likely compensating for the lower quality of information. This heightened response to uncertainty could also be interpreted as an orienting response (i.e. orienting the head or body towards the source of a stimulus; Sokolov, Nezlina, Polyanskiĭ, & Evtikhin, 2001). For instance, humans often reorient their head and/or body towards visual stimuli when they appear far from where their centres of acute vision are currently looking (Corneil, Munoz, & Olivier, 2007). Overall, our finding is consistent with other ecological conditions in which uncertainty is high, such as in visually obstructed habitats, where starlings become more vigilant (Devereux, Whittingham, Fernández-Juricic, Vickery, & Krebs, 2005).

The region of the visual field used to monitor neighbours can have implications for the spatial arrangement of individuals in a group. If birds monitor neighbours using the centres of their acute vision, assuming a frontolateral projection of the fovea, as is the case with starlings, then we would expect groups to have a circular arrangement with the beaks facing inwards. However, Bekoff (1995) found that grosbeaks were less vigilant and more responsive to changes in group size when in a circular arrangement than when in a linear arrangement. If birds monitor neighbours with their retinal periphery, assuming a retinal configuration similar to starlings, then we would expect groups to have a circular arrangement but with the beaks facing outside of the group. However, this arrangement may not be possible in contexts such as daytime or night-time roosts as they may require a linear arrangement (Feare, 1984). In this linear arrangement, if birds monitor neighbours with their retinal periphery, individuals would be expected to orient antiparallel to neighbours (i.e. every other bird's beak pointing in one direction). That is exactly what we found: starlings were quicker to react when their bodies were antiparallel than when they were in parallel positions. However, we acknowledge that this interpretation is preliminary because our study was limited to pairs of birds in a perching context, and thus, our findings do not extend to larger group sizes and other contexts. Daytime and night-time roosts are also often more spatially complex, with tree branches in parallel or in different orientations. In addition, thermoregulatory factors (e.g. wind direction and speed) are likely to affect the energetic costs of certain body orientations. These factors may determine whether starlings orient themselves in a way that allows them to monitor certain neighbours but not others.

Based on the effect sizes, sex composition of the pair appeared to be the main driver of spatial positioning with respect to neighbour distance and relative body orientation. Pairs of females tended to stand farther away and parallel to each other more often, and to orient the front of their heads towards each other more often, compared to pairs of males or mixed-sex pairs. The implication is that groups composed mostly of females might be more vulnerable to predators given that they may have the rear of their heads (i.e. blind areas) oriented towards the edges of the group, reducing the chances of detecting predators. Groups composed only of males, in contrast, would tend stand closer together and to have their visual fields facing towards their surroundings, potentially facilitating the detection of predators at the edges of a group.

Overall, our findings suggest that having a wide visual field may facilitate monitoring neighbours by reducing attention costs. Using areas with low visual resolution (i.e. retinal periphery) to monitor neighbours may free up the centres of acute vision for gathering other forms of information that require higher visual resolution (foraging, predator detection). Utilizing the retinal areas with low visual resolution also may allow starlings to monitor more group mates simultaneously due to their wide visual fields. Monitoring multiple individuals at once can increase the accuracy of escape decisions, leading to fewer false alarms (Proctor et al., 2003). Using this sensory perspective to understand how animals monitor each other can help us gain novel insights into the spatial distribution of animals within a group, the speed of information flow, and potentially the mechanisms behind collective behaviour.

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Supplementary Material

Supplementary Material associated with this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2016.08.002.

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