



# How do birds look at their world? A novel avian visual fixation strategy

Shannon R. Butler<sup>1</sup> · Jennifer J. Templeton<sup>2</sup> · Esteban Fernández-Juricic<sup>1</sup>

Received: 3 August 2017 / Revised: 26 January 2018 / Accepted: 1 February 2018  
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## Abstract

A central assumption in behavioral research is that the observer knows where an animal is looking; however, establishing when an animal is gazing (i.e., visually fixating on an object) has been challenging in species with laterally placed eyes. We quantitatively tested three fixation strategies proposed in the literature for birds, using European starlings (*Sturnus vulgaris*). We did not find strong support for any of the three strategies, despite high statistical *a priori* power (93%). However, we did observe a new visual fixation strategy that we labeled monocular alternating fixation. In this strategy, starlings moved their heads to make multiple fixations with a single eye before switching to the other eye and repeating the same process. Additionally, we established that individuals favored using the left over the right eye, supporting that laterality in starlings is left-eye dominant. The newly observed fixation strategy may be associated with the high level of intra-retinal variation (density of photoreceptors, overall sensitivity of visual pigments, etc.) in the starling retina. From a functional perspective, this monocular alternating fixation strategy may be beneficial to integrate the different types of information gathered by the different portions of each retina more quickly. We discuss the implications of our results for designing and interpreting behavioral experiments that require an understanding of where a bird is looking.

## Significance statement

This is the first study to quantitatively test three hypotheses in the literature about how animals with laterally placed eyes look at objects. We found that there was not strong support for any of these three strategies, but found support for a newly described strategy for birds to look at objects (i.e., multiple looks with a single eye before switching to the other eye).

**Keywords** Vision · Laterality · European starling · Fixation · Avian vision

## Introduction

A central assumption of some behavioral research is that the observer knows where an animal is looking. This is evident in

foraging behavior, anti-predator behavior, animal communication, social behavior, mate choice, parental care, etc. For instance, we measure female choice by establishing (among other things) how much time a female spends with a given male, but assuming that the female had visually explored each individual male before making her final decision. We measure risk taking behaviors in a predator-prey context by measuring the distance at which the prey escaped in response to an approaching predator, but assuming that the prey had spent time visually scanning the environment in the direction of the predator's approach and had detected it before initiating the escape. However, establishing what specific behaviors are associated with the direction an animal is looking at has been challenging (e.g., Treves 2000; Fernández-Juricic et al. 2004), particularly in species with laterally placed eyes as each eye projects to a point in space on a different side of the head (Davidson et al. 2014). The study of visual fixation strategies provides a venue to address this gap.

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Communicated by N. Clayton

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**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s00265-018-2455-0>) contains supplementary material, which is available to authorized users.

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✉ Shannon R. Butler  
shannon.rhey.butler@gmail.com

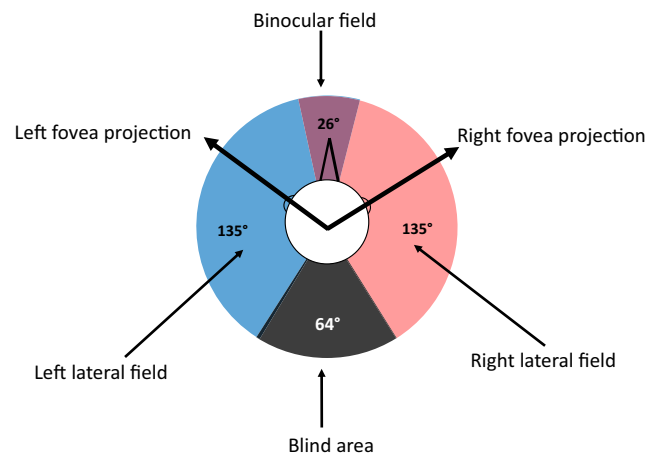
<sup>1</sup> Department of Biological Sciences, Purdue University, 915 West State Street, West Lafayette, IN 47905, USA

<sup>2</sup> Department of Biology, Knox College, 2 E. South St., Galesburg, IL 61401, USA

Visual fixation (i.e., maintaining gaze on an object) is a fundamental behavior that visually oriented animals use to gather information from their environment. Almost all vertebrates with a heterogeneous distribution of photoreceptors in their retinas fixate in some way by using specialized retinal areas that project into their visual fields (Land 2015). For instance, humans tend to orient their heads towards an object because they have frontally placed eyes and the specialized retinal areas are approximately at the centers of their eyes; hence, the projection of the head reflects the projection of acute vision. Because animals rarely have total visual coverage (i.e., 360° vision; Martin 2007), the need to fixate into different parts of their visual surroundings translates into different behaviors (eye movements, head movements, body movements; Land 1999a). These behaviors allow for the re-orientation of the eye into space to align the specialized portion of the visual field (i.e., acute vision, binocular vision, etc.) with the object of interest. Overall, fixation can be thought of as the process by which the brain collects information through the eyes (Diedrich and Schaeffel 2009; Larsson 2015).

Fixation strategies have been studied extensively in animals with frontally placed eyes (e.g., humans: Martinez-Conde et al. 2004; owls: Ohayon et al. 2008; non-human primates: Kano et al. 2012). However, fixation strategies have received relatively less attention in animals with laterally placed eyes (but see Lustig et al. 2012; Tyrrell et al. 2014; Katz et al. 2015). Birds are actually an excellent taxa to study fixation in vertebrates with laterally placed eyes because they are visually oriented (Martin 2007) and different species have different types of retinal configurations (Walls 1942), some of which are similar to humans. For instance, many songbirds have a single fovea with a high density of photoreceptors providing high visual acuity (Fernández-Juricic 2012). In most songbirds, the fovea from each eye projects into each lateral visual field, rather than the binocular field due to the lateral positioning of the eyes (Moore et al. 2015). Consequently, each lateral field has a single high-resolution visual input in songbirds. Although the binocular field has lower visual resolution, both eyes can see objects in this region simultaneously. Birds mostly move their heads in different planes, allowing the animal to expose different sectors of the visual field (i.e., lateral right, lateral left, binocular) to the object of interest. Consequently, avian head movements can be considered functionally similar to the eye movements in humans (Land 1999a).

Fixation strategies based on head movements have received some attention in the literature (Martinoya et al. 1984; Maldonado et al. 1988; Dawkins 2002) as a first level of assessment as to what birds are looking at. Three distinct head movement-based fixation strategies have been proposed for birds with laterally placed eyes (Fig. 1); however, they have never been tested simultaneously. First, birds can use a single fovea from either the left or right eye, locking the high-



**Fig. 1** Diagram of visual field of European starlings

resolution input for a certain time period with a lateral view of the object of interest (hereafter, monocular gaze-locking fixation strategy; Maldonado et al. 1988; Dawkins 2002; Fig. 2). Second, birds can use their left and right eyes alternately such that they receive the high-resolution input from both foveae, but not simultaneously (hereafter, biocular alternating fixation strategy; Dawkins 2002; Fig. 2). Using both eyes in succession may allow birds to engage both centers of acute vision (right and left) in information gathering since there is minimal information exchange between eyes in birds (Saleh and Ehrlich 1984; but see Templeton and Christensen-Dykema 2008). Third, birds can use their binocular field, locking the front of the head (and beak) towards the object for a given time receiving the visual input from both eyes simultaneously but at a lower visual resolution per eye (hereafter, binocular gaze-locking fixation strategy; Bloch and Martinoya 1982; Maldonado et al. 1988; Fig. 2). Please note that binocular refers to the use of the binocular field (Fig. 2), where both eyes can see simultaneously, whereas biocular refers to using both eyes (not necessarily at the same time using the binocular field, see Tyrrell et al. 2014).

Under the monocular gaze-locking and biocular alternating fixation strategies, one eye could be preferred over the other, leading to lateralization in visual fixation. Interestingly, some birds have a preference for one eye over the other or differences in performance abilities between the eyes (Rogers and Vallortigara 2013). This laterality has been shown in birds behaviorally (Rogers 2000; Franklin and Lima 2001; Templeton and Gonzalez 2004; Beauchamp 2013) and physiologically (Hart et al. 2000) and is particularly relevant because (almost) all the visual input from the left eye in birds goes to the right hemisphere and vice versa (Saleh and Ehrlich 1984; Rogers 2000; Voss and Bischof 2003).

This study had two main goals. First, we *quantitatively* tested the three head movement-based fixation strategies proposed in the literature using European starlings, a songbird whose visual system has been relatively well characterized

**Fig. 2** Predictions for the dimensions of fixations (the time between fixations, the angle of the head, the magnitude of the fixation, and the coefficients of variation in these three parameters) of the three hypothesized fixation strategies for birds. Green arrows represent a predicted increase and blue arrows represent a predicted decrease

	Monocular gaze-locking	Binocular gaze-locking	Biocular Alternating
Time between head movements mean	↑	↑	↓
Time between head movements variability	↓	↓	↑
Angle mean	↑	↓	↑
Angle variability	↓	↓	↑
Magnitude mean	↓	↓	↑
Magnitude variability	↓	↓	↑

(Martin 1986; Dolan and Fernández-Juricic 2010; Tyrrell et al. 2015). We did this by measuring the fixation strategy of a subject exposed to two treatments: stimulus present vs. stimulus absent. The stimulus absent treatment allowed us to characterize the baseline fixation strategy and then assess how it changed relative to having the stimulus present. We conducted these comparisons (stimulus absent vs. present) in two different scenarios: foraging (i.e., food present but no predator) and anti-predator (i.e., predator present but not food) to establish how generalizable our results were across contexts. However, we did not make comparisons between the foraging and anti-predator contexts. Second, we asked if the fixation strategy was lateralized (i.e., using one eye more than the other). European starlings have been shown to have lateralization in the distribution of cone photoreceptors (Hart et al. 2000) and in their ability to discriminate between stimuli (Templeton and Gonzalez 2004).

## Predictions

We made predictions so that we could distinguish between the three head movement-based fixation strategies (Fig. 2), using behavioral indicators of fixation patterns that are associated with changes in the orientation of the head and hence the eye (relative to visual scenes). We *operationally defined* a fixation as the period of time when the head remained still after a quick movement of the head. Specifically, the behavioral indicators that we used were as follows: (1) the time between fixations as an indicator of fixation duration (i.e., longer times mean longer time spent fixating), (2) the head angle relative to the object as an indicator of the portion of the visual field used

(i.e., higher values reflect higher chances of using either lateral field, lower values reflect higher chances of using the binocular field, see Fig. 1 for coordinate system), and (3) the magnitude of fixations (i.e., change in angle of the head) as an indicator of how different regions of the retina are used during fixation in successive fixations (i.e., higher values reflect higher chances of using different eyes, whereas lower values reflect higher chances of using the same eye). We also calculated the degree of variation (using the coefficient of variation) in each of these three parameters as it helped distinguish between the three fixation strategies (Fig. 2).

Under a monocular gaze-locking fixation strategy (Fig. 2), we predicted that there would be more time between fixations (with lower variation), higher head angle values (with lower variation), and smaller magnitude of fixations (with lower variation) when the object was present compared to when the object was absent. Under a biocular alternating fixation strategy (Fig. 2), we predicted that there would be less time between fixations (with more variation), higher head angle values (with more variation because of the alternation in the use of the eyes), and larger magnitude of fixations (with more variation) when the object was present compared to when the object was absent. Under a binocular gaze-locking fixation strategy (Fig. 2), we predicted that there would be more time between fixations (with lower variation), lower head angle values (with lower variation), and smaller magnitude of fixations (with lower variation) when the object was present compared to when the object was absent.

Additionally, since some fixation strategies (biocular alternating and monocular gaze-locking fixation strategies) could be dominated by one eye over the other (i.e., using one more

than the other), we predicted that the left eye would be used for a higher proportion of the fixations compared to the right eye because starlings have a relatively higher density of single cones (used for color perception and spatial resolution) in the left eye (Hart et al. 2000).

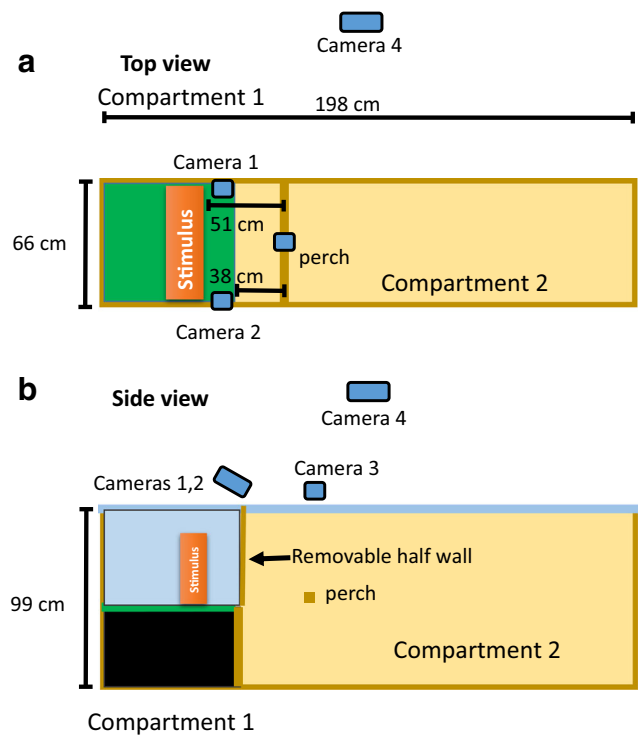
## Methods

We conducted this experiment from September 2014 through February 2015. We obtained the birds in December 2013 using modified decoy traps in Hamilton County, Ohio (N 39.2833, W 84.5947). We housed birds in aviaries (2.5 × 2.5 × 3.5 m) outdoors in mixed sex groups at the Ross Biological Reserve (Tippecanoe County, IN, N 40.4167, W 87.0693) and provided cat food, game bird maintenance chow, and water *ad libitum*. Several days before the trials, we moved the birds to enclosures indoors in groups of 2–4 to habituate them. The Purdue Institutional Animal Care and Use Committee (protocol 1306000876) approved all animal-handling procedures.

To determine our sample size, we conducted an *a priori* power analysis, calculating our effect size using a biologically relevant difference (the difference between the converged most position of the fovea and the edge of the binocular field at rest, 29°, according to Martin 1986), and an observed measure of variation in head angle from a pilot study ( $\sigma = 24.6^\circ$ ). We calculated power following Cohen (1988). We chose a sample size of 30 because it yielded over 93% power under these conditions (difference between mean tests with three groups and a calculated minimum detectable effect size ( $f$ ) of 0.48) for all mixed models (analyses on means and variation of time between fixations, angle, and magnitude).

Our experimental arena consisted of an enclosure that was 198 cm long by 66 cm wide and 99 cm high (Fig. 3a, b). The enclosure had a wooden frame and then was covered with foam board and butcher paper. The arena was divided in two compartments by a wall that was placed perpendicularly to the long edge of the arena (Fig. 3a, b). This wall was partially removable (the top half was able to be removed). Compartment 1 was 38 cm long, and compartment 2 was 166 cm long. Compartment 1 contained the experimental stimulus. The bird was in compartment 2, isolated from the stimulus. Compartment 2 contained a perch 50 cm above the ground 38 cm back from this removable wall (Fig. 3a, b).

We exposed 30 European starlings (16 males, 14 females) to three different stimuli in our experimental arena: a predator on a patch of grass (object present, predator), food on a patch of grass (object present, food), and an empty patch of grass (object absent). We had two exemplars of Cooper's hawks (*Accipiter cooperii*) as predators. One was perching (54 cm tall, 25 cm wide) and the other was in a soaring pose (66 cm wide, 13 cm tall at widest part of body). We hung the soaring



**Fig. 3** Dimensions of experimental arena from **a** a top view and **b** a side view

hawk from a thin wire attached to the top of the enclosure. We chose to use two different exemplars to avoid pseudoreplication (see Kroodsma et al. 2001). For food, we used a random selection of 20 dried mealworms (*Tenibrio molitor*, [tastyworms.com](http://tastyworms.com)) for each trial and spread them out on the grass in a circle of approximately 30 cm in diameter. For the object absent treatment, the background (grass, sky) was the same as in the previous two treatments but no predator or food was present.

A trial started with releasing a bird into the large compartment of the enclosure. The observer then hid out of sight and watched the bird on a computer screen that was connected to a DVR (Night Owl, H264 4-channel DVR). The DVR was connected to cameras, which the position of is illustrated in Fig. 3a, b. The observer then waited until the bird was perched with both feet oriented towards the removable wall for 5 consecutive s. After the bird was perched with the feet oriented forward for 5 s, we slowly removed the wall by sliding it down. The wall remained down for 30 s, or until the bird flew at the stimulus (whichever occurred first), at which time the trial ended. If the bird did not perch forward for 5 s after 15 min, the trial was terminated and attempted on a different day (i.e., criteria for unsuccessful trial). Each treatment was attempted twice per bird and one additional time at the end if the above criteria were not met. Because of these criteria, we ended up collecting data from 119 trials from 30 birds, 57 trials in the predator present treatment, 33 in the food present

treatment, and 29 in the object (predator or food) absent treatment. Please note that we did attempt to expose each bird to both models of the hawk once, rather than a single model twice. All birds were given one treatment per trial, in a random order, and only a single trial (and therefore treatment) per day. All 30 birds contributed to at least 1 food and 1 predator treatment, and 24 birds contributed to the empty condition.

The best proxy of fixation behavior is to track the movements of the eye and the projection of the fovea into the visual space using eye tracking technology, as has been done with primates (Guo et al. 2003). Despite the fact that eye tracking technology has been developed in birds (Yorzinski et al. 2013; Tyrrell et al. 2014), it is not yet developed to the point that we could use it to track their eye movements of small birds like songbirds while their heads move freely. This technological limitation led us to use head movements as a proxy of fixations as previous studies on birds have done (Land 1999b; Fernández-Juricic et al. 2013; Ochs et al. 2017).

Videos were coded using two programs: VirtualDub (<http://virtualdub.org/>) and Tracker (<http://physlets.org/tracker/>). Due to the need to synchronize the cameras with each other into a single video file, it was not possible to blind the coder from the treatment during coding. First, SRB identified each frame when the birds head became still after a movement (i.e., suggesting a fixation) using VirtualDub (at 30 frames per s). Then, an undergraduate student measured the angle of the head at each marked frame using Tracker. The undergraduate practiced using this program until she had sufficient reliability (i.e., could measure the same angle multiple times on the same video over time), being consistent with herself within 2° for 95% of fixations. We measured all fixation behavior that occurred within the first 5 s of perching time because we wanted to measure the bird's initial examination of the stimulus. If a bird left the perch before the 5 s, we resumed measuring up to 5 s of cumulative perching time, after the bird landed on the perch again. We did not consider head movements that were associated with landing and taking off in flight as fixations; thus, we only measured after/before the individual closed/opened its wings, respectively. For each fixation, we measured the position of the head (angle from above), magnitude of the fixation (by subtracting the angles of two consecutive head movements), and the time between fixations. We also calculated the coefficient of variation in the time between fixations, the head angle, and the magnitude of fixations for each trial.

We note that we did not project the gaze of the subject onto the stimulus; we simply measured the head movement patterns as a proxy of fixation behavior. Additionally, we do not make conclusions about what part of the stimulus the bird is fixating on (i.e., head, body, etc.), so the fact that our animals were not trained is not relevant (but see Qadri et al. 2016). Actually, the fact that our animals were not trained strengthens the ecological relevance of our conclusions due

to less of anthropogenic interference in the animals' responses compared to training.

**Data availability statement** All data analyses during this study are published in the [supplementary information](#) of this article.

## Statistical analyses

We ran general linear mixed models in SAS on the following dependent variables: the time between fixations, the head angle, the magnitude of fixation, and the coefficient of variation for each of the three aforementioned variables. Before running these models, we corroborated that our data was unimodal and roughly normal by visually inspecting it. We included the three treatments in the models, and when results from the overall model were significant (i.e., the F-statistics), we tested for the significance of the stimulus absent vs. present comparisons with Tukey tests (which yield t-statistics) to reduce the inflated chances of type I error associated with running multiple comparisons. For head angle, we used the absolute value of the head angle so that a high value would indicate the use of lateral vision and a low mean would indicate frontal vision. However, for the coefficient of variation, we did not take the absolute value since this would make the variation artificially low due to not accounting for negative values. Each of these six models contained the same independent variables: stimulus (predator, food, object absent), sex (male or female based on iris color according to Pyle 1997), body mass (g), and the interaction between stimulus and sex. We included these extra factors as covariates since they have previously been shown to affect behaviors in birds within a species (sex: Butler et al. 2016; Fernández-Juricic et al. 2013; body mass: Fernández-Juricic and Tran 2007; Jablonszky et al. 2017). Body mass can vary substantially within a sex, and there is much overlap in the distribution of body mass between sexes (Pyle 1997). We also included the interaction between treatment and sex because male and female vary their behavior in different contexts (Butler et al. 2016). We did not run any formal model selection process, but rather used a hypothesis-driven approach to construct our models as explained above. We ran the models using repeated measures to avoid pseudoreplication.

We note that we designed our experiment so that each context (predator, food) was compared to a control, but not to each other. The stimuli (food, predators) were different in terms of both the overall size and the expected behavioral responses (i.e., positive responses to food, fearful responses to predator) so comparing them directly could introduce some bias.

To assess if laterality occurred, we ran a mixed model with the proportion of fixations made with the left eye as the dependent variable and body mass (g), sex, and the interaction

between sex and treatment as independent variables, again repeated on individual.

## Results

### Fixation strategy

The time between fixations, the magnitude of the fixations, and the coefficient of variation in the time between fixations, coefficient of variation in the magnitude of the fixations, and the coefficient of variation in head angle were not significantly affected by the absence or presence of either object, the sex or body mass of the bird, or the interaction between sex and treatment (Table 1a, c–e, Fig. 4a, c–e). However, the angle of the head was significantly influenced by our treatments (Table 1b, Fig. 4b). More specifically, head angle values were higher when subjects were exposed to the predator compared to the object absent treatment ( $t_{37} = 3.38$ ,  $P = 0.0017$ ) and when exposed to the food compared to the object absent treatment ( $t_{37} = 3.33$ ,  $P = 0.0020$ ). These data are available in the electronic [supplementary material](#).

Overall, most of our results did not provide strong support for the three fixation strategies proposed (Fig. 2). This prompted us to take another look at the raw videos and made qualitative observations, which we describe for a few examples and provide supplemental videos here. In video S1, the bird was looking at some mealworms and made four fixations with the left eye, then 10 with the right eye, and then 1 with the left eye. In video S2, the bird was looking at a hawk and made 3 fixations with the right eye, 4 with the left, and then 7 with the right. In video S3, the bird made 5 fixations with the right eye and then 7 with the left. We plotted our data trial by trial (see examples in Fig. 5a–c), and upon visual inspection, we observed the same pattern as the videos showed: birds were making multiple fixations with a single eye and then switching to the other eye to make multiple fixations, and so on. This fixation pattern we observed can be actually deemed as a combination of the monocular gaze-locking and the biocular alternating strategies we tested originally (Fig. 2), although it leads to different predictions (see below). We decided to refer to this new fixation pattern we identified with these *post hoc* observations as monocular alternating, whereby birds tended to make multiple small magnitude fixations with a single eye aligned to the object of interest before aligning the opposite eye to the object of interest.

If birds were using the monocular alternating fixation strategy, they would be using the same eye to make multiple fixations in a row before switching to the other eye, leading to two quantitative predictions. First, there would be a significant and positive autocorrelation between successive head angles because birds would be more likely to use the same eye for the next fixation compared to using the opposite eye (which

**Table 1** The effect of treatment, body mass, sex, and the interaction between treatment and sex on: a the time between head movements, b head angle, c magnitude, d the coefficient of variation in the time between head movements, e the coefficient of variation in head angle, f the coefficient of variation in magnitude

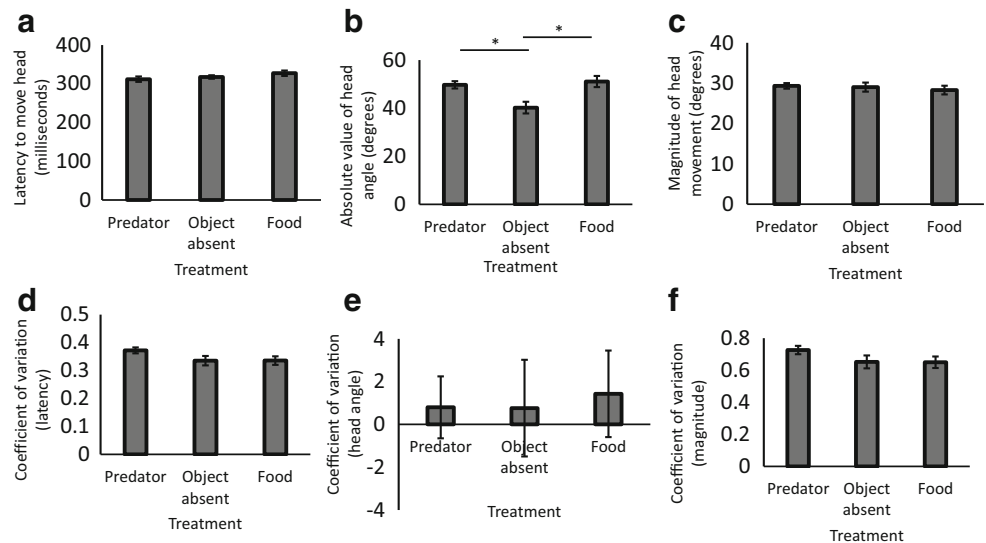
	<i>F</i>	<i>df</i>	<i>P</i>
<b>a</b>			
Treatment	1.81	2, 37	0.178
Body mass	0.05	1, 1647	0.831
Sex	3.91	1, 28	0.058
Treatment × sex	1.17	2, 37	0.321
<b>b</b>			
Treatment	<i>6.95</i>	2, 37	<i>0.003</i>
Body mass	1.73	1, 1647	0.189
Sex	2.06	1, 28	0.163
<b>c</b>			
Treatment	0.33	2, 37	0.724
Body mass	0.04	1, 1647	0.840
Sex	0.43	1, 28	0.515
Treatment × sex	0.95	2, 37	0.398
<b>d</b>			
Treatment	2.78	2, 37	0.075
Body mass	2.82	1, 91	0.097
Sex	0.04	1, 28	0.844
Treatment × sex	2.36	2, 37	0.109
<b>e</b>			
Treatment	0.04	2, 37	0.964
Body mass	2.82	1, 91	0.097
Sex	1.26	1, 28	0.272
Treatment × sex	0.04	2, 37	0.961
<b>f</b>			
Treatment	2.00	2, 37	0.149
Body mass	0.23	1, 91	0.633
Sex	2.25	1, 28	0.145
Treatment × sex	1.00	2, 37	0.377

Significant effects in italics

would result in a negative autocorrelation). Second, the number of fixations made before switching eyes would be significantly greater than 1 since they would be making multiple fixations with a single eye before switching to the other. We tested these predictions with our dataset. We indeed found a significant and positive autocorrelation between successive fixations (estimate = 0.84, Table 2c). Additionally, the 95% confidence interval of the number of fixations made in a row with one eye was significantly higher than 1 fixation (Fig. 6a).

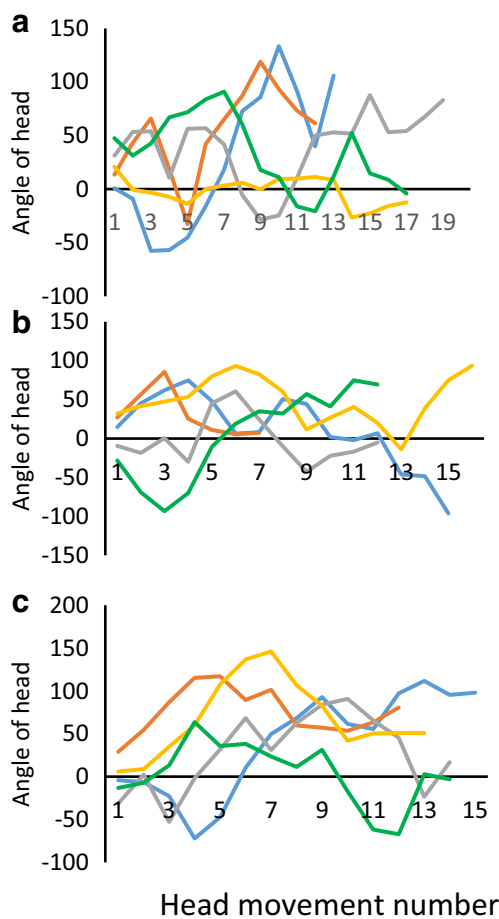
The aforementioned results suggest that the head movement behavior of the starlings used in this study fits the predictions of the monocular alternating fixation strategy. We then assessed whether individual birds would conform to this fixation strategy or not. We tallied each trial when a bird (1)

**Fig. 4** Effects of treatment (predator, food, object absent) on **a** time between fixations, **b** head angle, **c** magnitude of fixations, **d** coefficient of variation of the time between fixations, **e** coefficient of variation in head angle, and **f** coefficient of variation of the magnitude of fixations. All error bars represent SE. Asterisks and bars indicate statistically significant differences, with  $P < 0.05$



made multiple successive fixations with a single eye and (2) used both eyes within a trial. All (30/30) met both criteria in at least one trial. Additionally, in 127/127 trials, birds showed at least 2 fixations in a row with the same eye, and in 107/127 trials, birds used both eyes. We also assessed if the birds used

the strategy in both the predator and food contexts. In 33/33 food present trials, starlings made multiple successive fixations with the same eye, and in 23/33 of those trials, both eyes

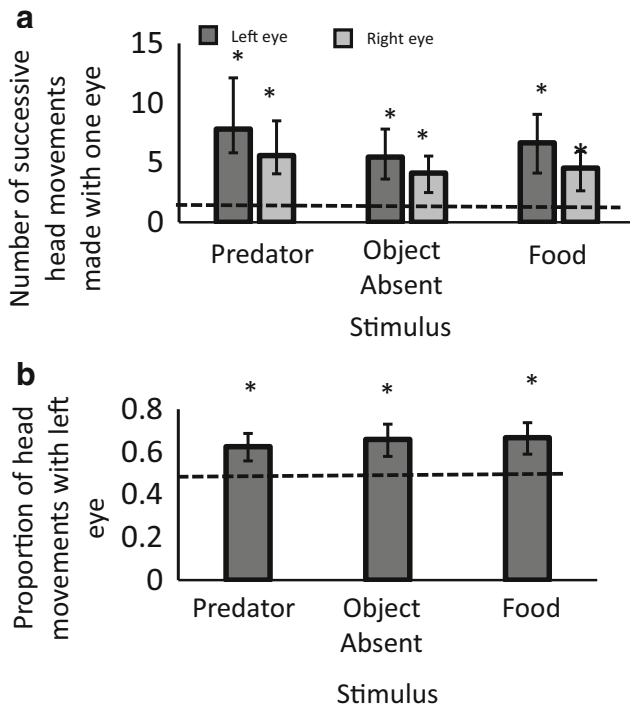


**Fig. 5** Examples of fixation patterns for **a** food, **b** predators, and **c** object absent. Each line represents a single trial

**Table 2** a The effect of treatment, body mass, sex, the interaction between treatment and sex, eye (left or right) and the interaction between treatment and eye on the number of head movements made in a row before switching to the other eye. b The effect of treatment, body mass, sex, the interaction between treatment and sex on the proportion of fixation made with the left eye. c Autocorrelation on head angle after controlling for body mass and sex

Number of head movements made in a row before switching eyes			
	<i>F</i>	<i>df</i>	<i>P</i>
<b>a</b>			
Treatment	3.16	2, 37	0.054
Body mass	1.55	1, 1644	0.213
Sex	0.44	1, 28	0.058
Treatment × sex	2.32	2, 37	0.112
Eye	8.28	1, 29	<i>0.007</i>
Eye × treatment	0.04	2, 30	0.960
Proportion of fixations made with the left eye			
	<i>F</i>	<i>df</i>	<i>P</i>
<b>b</b>			
Treatment	1.12	2, 37	0.337
Body mass	3.05	1, 1647	0.081
Sex	0.44	1, 28	0.513
Treatment × sex	4.05	2, 37	<i>0.026</i>
Autoregression head angle			
	<i>F</i>	<i>df</i>	<i>P</i>
<b>c</b>			
Head angle	2418.2	1, 1233	< 0.0001
Body mass	1.35	1, 1233	0.245
Sex	0.01	1, 96	0.939

Significant effects in italics



**Fig. 6** Effects of treatment (predator, food, object absent) on **a** the number of fixations made with each eye (left, right) before switching to the other eye and **b** the proportion of fixations made with the left eye. Error bars for **a**, **b** represent 95% confidence intervals. Dotted lines represent chance levels for **a** the number of fixations and **b** the proportion of fixations. Asterisks indicate a statistically significant difference from these chance levels, with  $P < 0.05$

were used. In 64/64 predator present trials, starlings made multiple successive fixations with the same eye, and in 59/64 of those trials, both eyes were used. Overall, it seems that most of the birds tested followed the monocular alternating fixation strategy in both contexts (foraging, anti-predator). These data are available in the [electronic supplement](#).

### Laterality

In terms of laterality, birds made significantly more fixations in a row with the left eye than with the right eye (Fig. 6a, Table 2a) in all treatments. They also used their left eye for a significantly higher proportion of fixations than expected by chance (Fig. 6b), and consequently, their right eye for a significantly lower proportion than chance.

### Discussion

Our findings suggest that starlings do not follow any of the three head movement-based fixation strategies (monocular gaze-locking, biocular alternating, binocular gaze-locking) previously proposed in the literature for species with laterally placed eyes (Fig. 2). Actually, our results on the variation in head angles and our *post hoc* analyses suggest that starlings

may use a different head movement-based fixation strategy, which we labeled as monocular alternating. We first discuss some potential reasons behind the lack of support for the previously proposed fixation strategies, and then the potential benefits of the monocular alternating fixation strategy given the configuration of the avian visual system.

One possibility for our inability to find support for the three previously proposed head movement-based fixation strategies could be because our experimental manipulations were insufficient to elicit a substantial fixation response. However, our birds did vary the angle of their head when there was an object present compared to when it was absent, which suggests that our manipulations did elicit head movement responses. Alternatively, our sample size may have been too small to detect an effect; however, our power estimates (93%) suggest otherwise. Another possibility is that we may not have measured a sufficient duration of time when the birds were actually gathering information. However, we conducted an analysis on a previously published experiment with starlings (Templeton and Christensen-Dykema 2008) to establish how many fixations individuals would make in a foraging context (see [supplementary material](#)). We found that starlings tended to make a similar number of fixations before making a decision (i.e., whether to peck or not) as the number of fixations we measured in our experiment (two sample  $t$  test,  $t_{46} = 0.753$ ,  $p = 0.228$ , [supplementary material](#)). We then believe that our manipulations were appropriate, but the reason our predictions were not fully supported was probably because the fixation strategy starlings used was different from previously proposed ones. Additionally, although our stimuli differed in size, we do not believe this affected our findings. For instance, the head angle did not differ between the two hawk models ( $F_{1,14} = 0.52$ ,  $P = 0.482$ ) that differed in size. Finally, the set of *post hoc* predictions we made (autocorrelation, number of fixations before switching eyes) did positively support our newly observed fixation strategy.

The new fixation strategy can be characterized as follows: birds make multiple fixations with only one eye before switching to the other eye to make multiple fixations with it. To some extent, this new fixation strategy may seem a combination of the biocular alternating and monocular gaze-locking strategies. However, there are two key components that clearly distinguish monocular alternating from the other fixation strategies (Fig. 2). First, the number of fixations made before switching to the opposite eye is significantly greater than 1. These small head movements could function to allow birds to use multiple parts of their retina to look at an object (see below). Actually, this is supported by the fact that the avian retina is heterogeneous (i.e., intra-retinal variation) morphologically (i.e., density of photoreceptors, absorbance of visual pigments, etc.) and thus functionally (reviewed in Temple 2011). Second, after multiple fixations with one eye, birds *also* switch to the other eye (Figs. 5a–c and 6a), which is



contrary to the predictions for any of the strategies illustrated in Fig. 2. This may allow individuals to gather information from an object from the perspective of *both* eyes. Therefore, birds may have two layers to integrate information: within-eyes and between-eyes. We speculate that the monocular alternating strategy may facilitate the integration of spatial information because successive snapshots taken from small magnitude head movements will have more overlap between them than those from large magnitude head movements. Having the second eye do the same may help birds “line-up” different regions of the environment and compensate for the limited information flow between the left and right brain hemispheres (Saleh and Ehrlich 1984; Templeton and Christensen-Dykema 2008).

Our findings support the preference for one eye over the other (i.e., behavioral inter-retinal differences). This behavioral result can be linked to differences between the eyes. Starlings have a higher concentration of single cones (used for chromatic perception) in their left eye compared to their right (Hart et al. 2000), which may enhance visual resolution and chromatic contrast in certain regions of the spectrum. Starlings made more fixations with their left eye oriented towards the stimulus before switching to the right eye than in the opposite scenario (i.e., viewing with the right eye and then switching to the left). One of the implications is that starlings may position themselves in a way that could optimize the use of the dominant eye for one task over the other, like foraging or searching for predators. For example, sandpipers are more successful when they use their right eye to look for predators and presumably their left eye to forage (Beauchamp 2013). Dark eyed juncos also favor their right eye for vigilance (and presumably the left eye for foraging), but tree sparrows do not prefer one eye over the other (Franklin and Lima 2001).

Our results provide novel insights into the behavioral mechanisms that species with laterally placed eyes use to gather visual information through head movements. One of the limitations of our and previous studies on head movement-based fixation strategies (Fig. 2) is that eye movements were not considered, despite the fact that they can be important in birds (e.g., Tyrrell et al. 2015). However, a study that would take into account the movements of both eyes simultaneously and the head would require eye tracking technology that has yet to be developed (i.e., current eye trackers can either record only eye with the head moving (Yorzinski et al. 2013) or both eyes with the head restrained, Tyrrell et al. 2014).

Starlings appear to use multiple fixations to expose different parts of a single retina to the object of interest before switching to the other eye, which may be necessary to gather multiple types of information (chromatic, achromatic, motion, etc.). However, other taxa appear to show different fixation strategies (Fig. 2). Species with frontally placed eyes tend to use binocular gaze locking in most situations (e.g., humans: Martinez-Conde et al. 2004, other primates: Guo et al. 2003;

Kano et al. 2012, owls: Ohayon et al. 2008). Among species with laterally placed eyes, pigeons tend to use binocular gaze-locking to track a stimulus when it is moving slowly or is close by, but monocular gaze-locking when the stimulus is moving faster or is farther away (Bloch and Martinoya 1982; Maldonado et al. 1988). Chickens tend to use binocular gaze-locking to view close objects, but biocular alternating to view far objects (Dawkins 1995, 2002). Finally, gull-billed terns appear to use monocular gaze-locking while hunting (Land 1999b). It is unclear at this point what accounts for this diversity in fixation strategies; however, a recent study showed an association between the degree of inter-specific variation in the configuration of the avian retina (i.e., changes in spatial resolving power across the retina) and head and eye movement behaviors (Moore et al. 2015).

Our results have implications for improving our ability to estimate what a bird is looking at. From a video collection perspective, top-view cameras would facilitate establishing whether or not birds follow the monocular alternating strategy by recording changes in the orientation of the head relative to plane between a given object and eyes. From an inference perspective, our results provide a set of predictions relative to specific patterns of head movement if birds engage in fixation behavior (i.e., exploring visually a particular object) as opposed to scanning the environment without focusing on any given object. However, to establish the direction of the fixation (i.e., which specific object is being investigated visually) requires extra information, such as the location of the retinal center of acute vision to project it in the visual space based on the position of the head relative to objects of interest (using top-views) (e.g., Butler and Fernández-Juricic 2018). This approach can provide a new layer of understanding as to what birds are looking at but it is still not as accurate as using eye tracking technology to measure visual attention (e.g., Tyrrell et al. 2014). Additionally, some researchers have used peep-holes to determine whether an animal is paying attention (Grodzinski et al. 2012; Shaw and Clayton 2013; Butler and Fernández-Juricic 2014) to a given object, which is a good alternative to determine *where* an animal is looking at if the location of the retinal center of acute vision is unknown. However, an animal may remain close to peep hole for numerous reasons besides looking at the stimulus, such as trying to be near cover or an escape path. With this new fixation strategy, we could increase our ability to determine if they are actually *looking through* the peep hole as opposed to *being near* the peep hole. Finally, our results raise some interesting questions about the ecological implications of this new fixation strategy. This monocular-alternating strategy results in more head motion than other strategies (e.g., gaze-locking). Could predators use this increase in prey head motion as a cue that to break prey crypsis (e.g., Forsman and Appelqvist 1998) or to estimate when prey may be more vulnerable because their attention are more focused on foraging rather than

vigilance? Could conspecifics use this head movement strategy as an indicator of where an animal is paying attention to follow gaze (e.g., Loretto et al. 2010; Schmidt et al. 2011; Butler and Fernández-Juricic 2014) or anticipate food finding and eventually steal food (e.g., scrounger tactics)? Addressing these questions will enhance our understanding of the relationship between visual configuration and visual behavior.

**Acknowledgements** We would like to thank three anonymous reviewers or their helpful comments. Hannah Smith (HS) was very helpful in collecting the data from the videos. We are grateful to the USDA APHIS in Ohio who provided the starlings for this experiment, as well as Tom Gnoske from the Field Museum of Natural History in Chicago, IL, who graciously prepared and donated one of our Cooper's hawk models, and Dr. Barney Dunning from the Department of Forestry and Natural Resources at Purdue University for allowing us to borrow another Cooper's hawk model.

**Funding** This research was funded by Animal Behavior Society grant to SRB, a Purdue Research Foundation grant, and a National Science Foundation Grant IOS 1146986. The experiment in the [supplementary material](#) was financially supported by the Knox College Richter Fund and National Science Foundation Grant IBN 0109024.

## Compliance with ethical standards

**Ethical approval** The Institutional Animal Care and Use Committee of Purdue University (protocol 1306000876) approved all animal-handling and care procedures. 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; United States Department of Agriculture, APHIS, Wildlife Services). For the experiment in the [supplementary material](#), procedures were approved by the Institutional Animal Care and Use Committee of Franklin & Marshall College (Protocol # 2000-05).

**Conflict of interest** The authors declare that they have no conflict of interest.

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