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RESEARCH ARTICLE

Oculomotor strategy of an avian ground forager: tilted and weakly yoked eye saccades

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ABSTRACT

Many bird species are capable of large saccadic eye movements that can result in substantial shifts in gaze direction and complex changes to their visual field orientation. In the absence of visual stimuli, birds make spontaneous saccades that follow an endogenous oculomotor strategy. We used new eye-tracking technology specialized for small birds to study the oculomotor behavior of an open-habitat, ground-foraging songbird, the European starling (*Sturnus vulgaris*). We found that starlings primarily move their eyes along a tilted axis 13.46 deg downwards anteriorly and upwards posteriorly, which differs from the axis parallel to the horizon employed by other species. This tilted axis could enhance foraging and anti-predator strategies while starlings are head-down looking for food, allowing them to direct vision between the open mandibles to visually inspect food items, and above and behind the head to scan areas where predators are more likely to attack. We also found that starlings have neither fully conjugate saccades (as in humans, for example) nor independent saccades (as in chameleons, for example). Rather, they exhibit weakly yoked saccades where the left and right eyes move at the same time but not at the same magnitude. Functionally, weakly yoked saccades may be similar to independent saccades in that they allow the two eyes to concomitantly perform different tasks. The differences between the oculomotor strategies of studied species suggest eye movements play variable but important roles across bird species with different ecological niches.

KEY WORDS: Visual field, Sensory, Vision, Bird, *Sturnus vulgaris*

INTRODUCTION

Birds move their heads and eyes in a saccadic fashion (Land, 2015). Head and eye saccades are functionally relevant because they facilitate the inspection of different visual targets in the environment (Land and Nilsson, 2002). Although past literature has deemed eye movements as limited in birds (Jones et al., 2007), recent studies have demonstrated that this is not the case across Passeriformes, as well as some non-Passeriformes (Fernández-Juricic et al., 2008; Martin, 2009; Moore et al., 2013). Birds commonly use head movements to make simple changes in gaze direction (Land, 2015). Eye saccades are used not only to relocate gaze but also to modify the configuration of the visual field. For example, birds can converge their eyes to increase the degree of binocular overlap in front of the head (Martin, 1986), which could have consequences for foraging behavior (Moore et al., 2015). Divergent eye saccades reduce the size of the blind area behind the head, increasing visual coverage around the head (Martin, 1986) and hence the chances of detecting threats (Fernández-Juricic et al., 2004). Besides these two types of conjugate eye saccades, movements of the left and right eyes could occur independently of one another, suggesting the animal may view the world diplopically (i.e. viewing two separate locations simultaneously) or with attention directed to only one eye at a time (Martin, 2014). Avian eye saccades are also known to serve other important functions, such as gaze stabilization during locomotion (Land, 2015). Additionally, it could be beneficial for stalking predators, like herons, or hidden prey to use eye saccades rather than head movements to search the environment because eye saccades create a less conspicuous motion cue for enemies to detect.

Even in the absence of visual stimuli, animals make saccades spontaneously in a definable pattern that follows an endogenous oculomotor strategy (Wallman and Pettigrew, 1985). Oculomotor strategies generally include a primary gaze position that may serve several functions, including reducing fatigue or energetic costs and keeping the eye in a position that can reach important locations of the visual field with a single saccade (Wallman and Pettigrew, 1985). It is possible that animals capable of large degrees of eye movement, such as Passerines, expand the primary gaze position to also execute spontaneous saccades along a primary gaze axis. This could be driven by the reduced cost of only investing resources in musculature, innervation and control mechanisms to execute saccades along a single primary axis rather than investing in extra resources to execute saccades equally in all directions. Most ecologically important visual targets occur at predictable locations within the visual field (Hughes, 1977; Tyrrell et al., 2013). Therefore, a single well-developed primary saccade axis would be able to visually cover most ecologically relevant tasks at a reduced cost.

The configuration of the retina could also be important in shaping oculomotor strategies (Land, 2015). Regions of the retina with a higher density of photoreceptors (hence, higher spatial resolution) are known as centers of acute vision, which differ in type and number in birds (Collin, 1999). For example, hawks have two foveae (i.e. concentric increase in photoreceptor density with an invagination of the retinal tissue) per eye. One fovea projects laterally for monocular viewing and the second fovea projects binocularly (Reymond, 1985). In contrast, many birds have just a single fovea or a single area centralis (i.e. a concentric increase in photoreceptor density but without retinal invagination) (e.g. Dolan and Fernández-Juricic, 2010; Moore et al., 2013; Tyrrell et al., 2013).

The relationship between retinal configuration and spontaneous eye saccades has been investigated in some avian species. For example, chickens (*Gallus gallus*) have predominantly horizontal saccades that move their area centralis along the horizon (Schwarz et al., 2013). Zebra finches (*Taeniopygia guttata*) have both a central fovea and temporal area (Voss, 2005). In this case, both the axis

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between the fovea and the area and the axis of eye movement are aligned with the horizon (Voss and Bischof, 2009). Pigeons (*Columba livia*), which have a central fovea and a dorso-temporally shifted area, have a more complex pattern of eye movement (Bloch et al., 1984). Pigeons make saccades posterior to the resting position of the eye (i.e. back of the head) on an axis aligned with the horizon, but they direct saccades made anterior to the resting position of the eye (i.e. front of the head) downwards toward the beak tip (Bloch et al., 1984; Lemeignan et al., 1992). Presumably, posterior saccades are horizontal to view the more distant horizon with the fovea, whereas anterior saccades are downward to view the ground or beak with the dorso-temporal area prior to and during pecking (Bloch et al., 1984; Martinoya et al., 1984).

The degree of yoking between the two eyes is a component of the oculomotor strategy that shapes what saccades are used for (Land, 2015). In birds, the left and right eyes are often assumed to move independently of one another (Martin, 2009) similar to chameleon saccades (Ott, 2001). Yet, empirical studies have found a large amount of variation in the degree to which the two eyes are yoked together. Pigeons, for example, use fully yoked (i.e. conjugate) saccades for frontal viewing but independent saccades for lateral viewing (Bloch et al., 1984). Functionally, yoked saccades maintain a constant relationship between the two eyes, potentially allowing the brain to perceive a joint panoramic visual field rather than separate left and right hemifields (Voss and Bischof, 2009). Independent saccades, in contrast, release the two eyes from restricting one another's movement patterns, allowing them to concomitantly execute alternative tasks. Other species show different patterns. The eyes of the tawny frogmouth (*Podargus strigoides*) and little eagle (*Hieraaetus morphnoides*) are weakly yoked (Wallman and Pettigrew, 1985), whereas zebra finch eyes are strongly yoked (Voss and Bischof, 2009).

Furthermore, it is often implicitly assumed that, in birds, one eye can move to its maximum extent regardless of the direction in which the opposite eye is moving. However, this is not the case in humans, who cannot move both eyes to the outside corners of the eye socket simultaneously. The assumption that avian eye movements are not constrained in a similar fashion has never been empirically tested, but it is prevalent in the study of avian visual fields (size of the binocular field, lateral fields and blind area) (Martin, 1986). Visual fields are often measured with the eyes in three different stages: converged, at rest and diverged. Because visual fields are measured on one eye at a time, the opposite eye is assumed to be in the same forward or backward position. However, if this assumption is not correct, then our functional interpretations of binocular field and blind area plasticity could change.

Our goal was to investigate for the first time three components of the oculomotor strategy of a ground-foraging bird with a single laterally projecting fovea, the European starling (*Sturnus vulgaris* Linnaeus 1758). (1) The presence and orientation of the primary saccade axis. The horizon is a particularly important feature for animals living in open habitats, such as starlings, because predators and conspecifics must appear within a few degrees of the horizon when there is little visual obstruction in the habitat (Hughes, 1977). Therefore, we predicted that starlings would have a primary gaze position axis parallel to the horizon, which would allow them to scan the entire horizon with their fovea. (2) The degree of yoking between the starling's left and right eyes. (3) We tested the assumption that starlings have the ability to fully converge and diverge their eyes. We used novel, non-invasive eye-tracking technology because it can accurately track gaze position, which is more precise than recording eye position alone (Tyrrell et al., 2014).

RESULTS

We found that, in the absence of visual stimuli, European starlings tended to move their eyes along an axis that was tilted 13.46 deg (mean resultant length $\bar{R}=0.99$, $N=12$, 95% CI=10.77 to 15.74 deg) downwards anteriorly and upwards posteriorly relative to the beak axis (Fig. 1). The starling beak axis is parallel to the ground during a typical head-up posture. Starlings made significantly more (Fig. 1B; $F_{1,69}=48.64$, $P<0.001$) and larger (Fig. 1D; $F_{3,32}=8.22$, $P<0.001$) spontaneous saccades in the dorso-temporal and ventro-nasal directions than in the dorso-nasal or ventro-temporal directions. There was no significant difference between the slope of the saccade axis of the left and right eyes ($R=0.12$, $P=0.968$, $N=12$). There was also no effect of sex on saccade rate ($F_{1,22}=0.42$, $P=0.526$) or magnitude ($F_{1,10}=1.11$, $P=0.317$).

We found that the axis of movement when the bird's eye was in front of the resting position did not differ from the axis of movement behind the resting position ($R=0.59$, $P=0.352$, $N=12$). Additionally, we found that starlings were not more likely to look at food stimuli that were on the axis (probability of 0.67±0.16) compared with food stimuli presented off the axis (0.44±0.17, $F_{1,16}=0.83$, $P=0.375$).

The degree to which the two eyes are yoked together was significantly different from random ($d_{max}=0.101$, $d*_{n=710,}$ $_{\alpha=0.05}=0.072$, $P<0.05$, Kolmogorov–Smirnov test, $N=12$, bin width=0.05). In Fig. 2A, relative saccade amplitudes near a value of 1 would indicate strongly yoked saccades, whereas smaller values would indicate weakly yoked saccades and true zero values would indicate independent saccades. Starlings made significantly more saccades with relative amplitudes of 0–0.25 compared with relative amplitudes of >0.05–0.75 and >0.75–1.0 (Fig. 2A). Additionally, individuals made more saccades with relative amplitudes of >0.25–0.5 compared with saccades with relative amplitudes of >0.75–1 (Fig. 2A). Fig. 2B,C shows an example saccade path, highlighting the simultaneous onset of saccades in the left and right eyes. Overall, the distribution trended towards weakly yoked eye movements: the eyes moved at the same time, but their movements were not always of the same magnitude.

We found that starlings could fully converge their eyes (Fig. 3B, C). There was no significant difference between the maximum forward position of a convergent state versus a clockwise state ($t_{11}=2.04$, $P=0.066$; Fig. 3B) or a counter-clockwise state ($t_{11}=1.17$, $P=0.267$; Fig. 3C). Conversely, starlings were limited in their ability to fully diverge their eyes (Fig. 3A,D). Starlings were able to move both eyes backwards at the same time, but the magnitude of such movements was smaller than if only one eye moved backward. For example, the left eye could move further backward when both eyes moved counter-clockwise compared with when both eyes diverged ($t_{11}=2.75$, $P=0.019$; Fig. 3A). This result was also observed for the right eye's ability to move backward ($t_{11}=5.35$, $P<0.001$; Fig. 3D). Finally, starlings were not more or less likely to make convergent or divergent saccades (0.50±0.05 saccades s^{-1}) than clockwise or counter-clockwise saccades (0.44±0.07 saccades s^{-1}; $t_{11}=0.68$, $P=0.510$). This indicates that starlings frequently make same-direction saccades and opposite-direction saccades.

DISCUSSION

In open habitats, foraging opportunities, predators, conspecifics, etc., tend to appear along the horizon (Hughes, 1977). A horizontal eye movement axis, which has previously been found in chickens (Schwarz et al., 2013) and zebra finches (Voss and Bischof, 2009), would allow birds to keep their centers of acute vision along the prominent horizon. However, contrary to our expectations, we found that European starlings primarily move their eyes along a
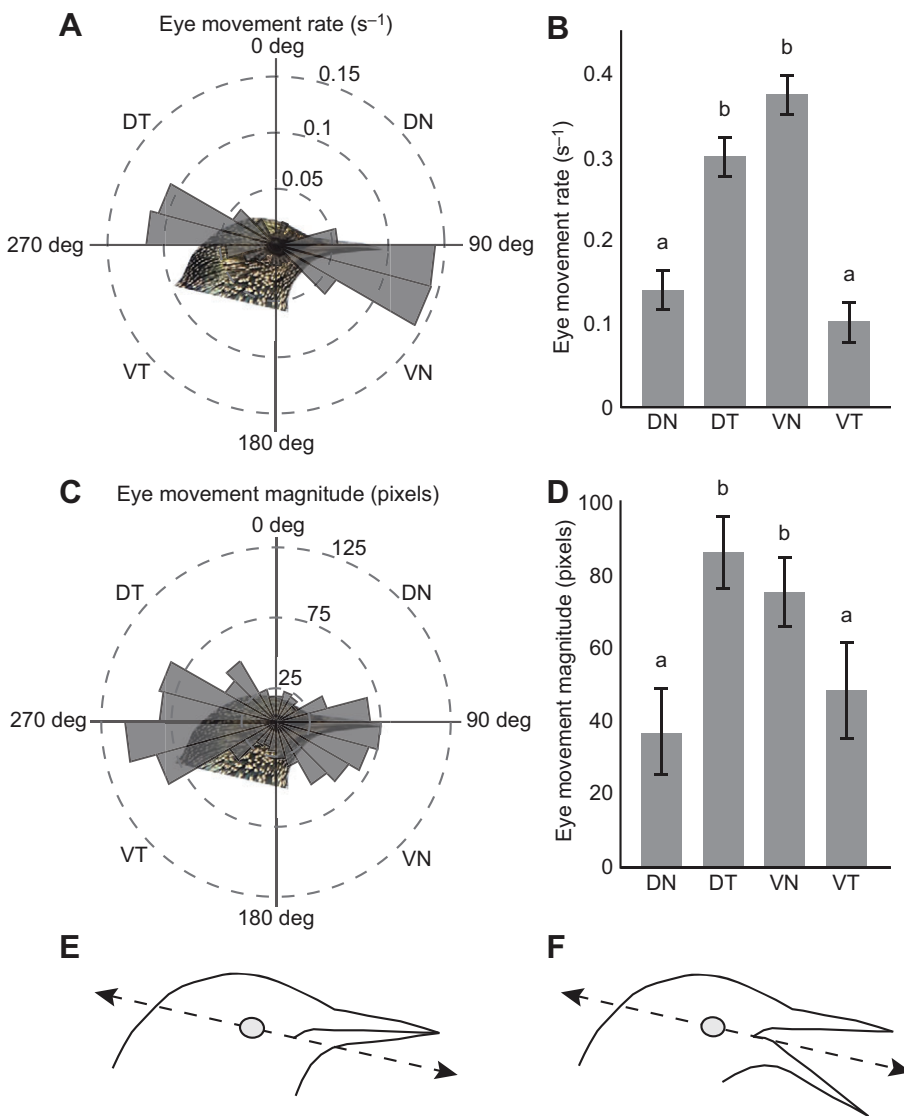
Fig. 1. Patterns of spontaneous saccades in European starlings. Dorso-temporal (DT), dorso-nasal (DN), ventro-nasal (VN) and ventro-temporal (VT) directions are abbreviated throughout. (A) Saccade rate (s^{-1}), binned into 15 deg wedges around the starling's head. Longer wedges indicate saccades were made more frequently in that direction. Concentric circles represent increasing saccade frequency, moving outwards. (B) Starlings move their eyes at a higher rate in the DT and VN quadrants compared with the DN and VT quadrants. (C) Average saccade magnitude (pixels) in 15 deg bins around the starling's head. Concentric circles represent increasing saccade magnitude, moving outwards. (D) Starlings' average saccade magnitude is higher in the DT and VN directions than in the DN or VT directions. Different lowercase letters indicate significant pairwise comparisons. (E) Mean eye movement axis at 13.46 deg off horizontal with a closed beak. (F) Mean eye movement axis with an open-bill probing position.

tilted axis (13.46 deg) (Fig. 1). Pigeons use a similar tilted axis when making forward saccades towards the beak, but the saccades made behind the eye's resting position occur along the horizontal (Bloch et al., 1984). Unlike any other bird species described, starlings have a single tilted axis of eye movement for eye saccades made in front and behind their eye resting position.

The unique oculomotor strategy of starlings may be a sensory specialization to suit the visual demands imposed by their foraging requirements and anti-predator strategy. Starlings are ground foragers with a specialized foraging technique (open-bill probing) (Beecher, 1978) that would require the visual inspection of food in the mandibles (Martin, 1986). A forward eye movement along the tilted axis would actually drive the eye towards the open space between the mandibles for visual identification and manipulation of newly exposed food items (Fig. 1E,F). This very directional eye movement could not be accomplished with a horizontal oculomotor strategy, as found in other species (e.g. Schwarz et al., 2013). Furthermore, when head-down probing, the tilted eye movement axis would also allow starlings to direct their vision above and behind the head, which is the most likely direction for aerial predators to approach ground-foraging prey (Lima, 1993). Therefore, the starling oculomotor strategy could enhance the

visual inspection of foraging opportunities and potential threats in a body posture (head-down) that reduces the chances of predator detection in open habitats (Tisdale and Fernández-Juricic, 2009).

The oculomotor strategy of starlings constrains the direction of spontaneous saccades, but not necessarily visual performance. When starlings were presented with a food stimulus in the dorso-nasal portion of the visual field, a region off the tilted axis of eye movement, they did not differ significantly in their likelihood to fixate on the stimulus compared with one that appeared within the primary axis of movement. Therefore, starlings are capable of making targeting saccades to other parts of the visual field when objects of interest appear, such as prey and predators (Tyrrell et al., 2014). Head movements could also be important for visual targeting under such viewing conditions. Head movements are responsible for 66–90% of gaze redirections in peafowl (*Pavo cristatus*) and pigeons (Gioanni, 1988; Land, 2015; Yorzinski et al., 2013). While starlings are capable of a greater degree of eye movement than either pigeons or peafowl, head movements certainly play an important role in gaze redirection. In fact, starling head movement rates (1.4–1.7 movements s^{-1}; Butler and Fernández-Juricic, 2014) are slightly higher than the eye movement rate in this study (1.0 saccades s^{-1}). The question that should be addressed in the
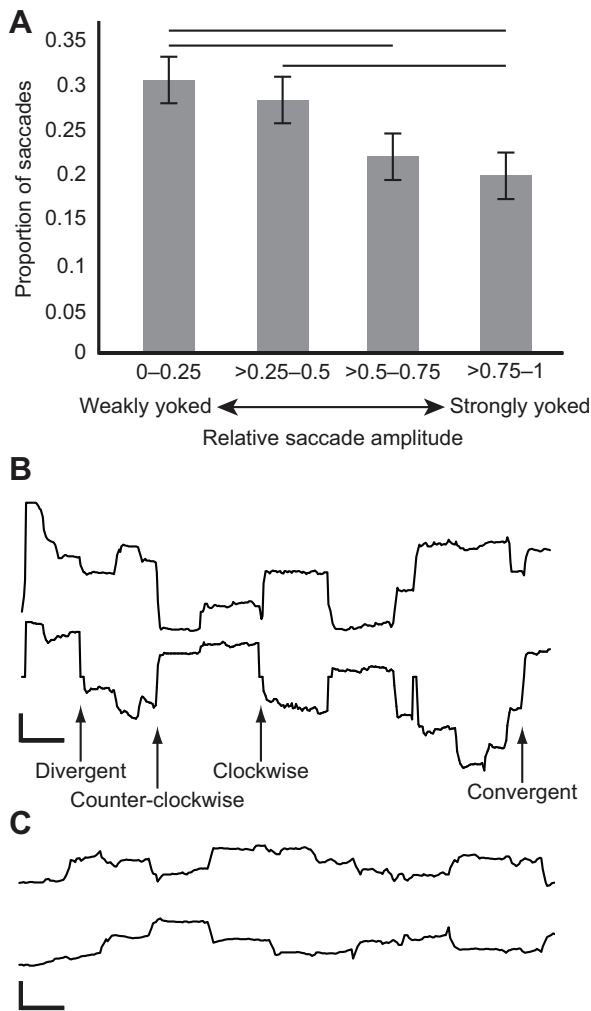
Fig. 2. European starling saccades are weakly yoked. When one eye moves, the other eye also moves, but not to the same degree. (A) The relative amplitude of spontaneous saccades made by the left and right eye in European starlings. Horizontal bars denote significant differences between bins. (B,C) Example saccades from one individual showing that saccades of the left and right eyes occur simultaneously. B shows eye position through time in the horizontal dimension. Arrows mark examples of the four different types of saccade combinations. Both traces moving up indicates a convergent movement, traces moving down indicates a divergent movement, traces coming together indicates a counter-clockwise movement, and traces spreading apart indicates a clockwise movement. C shows eye position through time in the vertical dimension. In each case, the top trace corresponds to the left eye and the bottom trace to the right eye. The vertical scale bars represents 10 deg and the horizontal scale bars represent 1 s.

Fig. 3. Starlings can fully converge their eyes, but they cannot fully diverge their eyes. Starlings can fully converge their eyes (B,C), but cannot fully diverge their eyes (A,D). Solid lines indicate mean foveal projection at maximum eye positions and lighter wedges indicate standard error. Red corresponds to a clockwise state where the left eye is positioned maximally forward while the right eye is positioned maximally backwards. Blue corresponds to a counter-clockwise state. Green corresponds to a converged state where both eyes are positioned forward. Black corresponds to a diverged state where both eyes are positioned backwards. Dashed lines indicate the resting position of the fovea projection. Asterisks indicate significant paired *t*-tests. ns indicates non-significance.

and Bischof, 2009). Functionally speaking, weakly yoked saccades could actually be deemed similar to independent saccades. Weakly yoked saccades may provide a mechanism by which foveate birds, like starlings, make simultaneous saccades to target two separate points of interest. Many birds have a single fovea in each eye (Dolan and Fernández-Juricic, 2010; Moore et al., 2013; Tyrrell et al., 2013), and because birds have laterally placed eyes, the two foveae project to different points on either side of the head. The divergent fovea projections introduce the possibility of the bird looking with high visual acuity in two places at once, something that humans cannot do because both eyes are directed towards the same point at all times. Fully yoked saccades would result in one eye making a targeting saccade to a point of interest while the opposite eye made a concomitant saccade towards a random point in the environment. Weakly yoked saccades, in contrast, would allow the bird to view one point of interest in the left visual field and a separate point of interest in the right visual field.

In terms of visual attention, it is likely that birds can only attend one eye at a time (Voss and Bischof, 2003), but how birds split attention time between the two eyes is still unknown. Despite the likelihood that birds cannot attend opposite points of interest simultaneously, weakly yoked saccades could still save time during vigilance behavior if they alternate attention between the two eyes at regular intervals, a tactic employed by chameleons (Ott et al., 1998). The equivalent visual search coverage with fully yoked saccades would require two sets of saccades – the first set to inspect a point of interest with one eye while the opposite eye moves to a random point of non-interest, and a second set to inspect an alternative point of interest with the second eye. The starling's weak yoking strategy, in contrast, could move the second eye to its point of interest with the first set of saccades. By reducing the number of required saccades, and thereby reducing the amount of time that vision is disrupted or impossible because of oscillations within saccades (Land, 2015; Wallman and Letelier, 1993), weakly yoked saccades could potentially be more time efficient than fully yoked saccades.

We found that starlings can fully converge their eyes (Fig. 3B,C). That is, they have the ability to swing both eyes forward simultaneously to the maximum extent that each eye is capable of individually, despite not reaching a state where the fovea is directed

future is how this oculomotor strategy interacts with the patterns of head movements that starlings use when gazing.

Our results show that starling eye movement patterns are neither fully independent (e.g. chameleons) nor fully conjugate (e.g. humans). Actually, their eye saccades can be considered intermediate between these extremes, or weakly yoked. When one eye makes a spontaneous saccade, the opposite eye makes a saccade at the same time but of a different magnitude (Fig. 2). Similar weakly yoked saccades have also been found in phylogenetically distant species within Accipitriformes and Caprimulgiformes (Wallman and Pettigrew, 1985). However, the weakly yoked saccades are different from the conjugate or strongly yoked saccades present in other Passeriformes, like the zebra finch (Voss
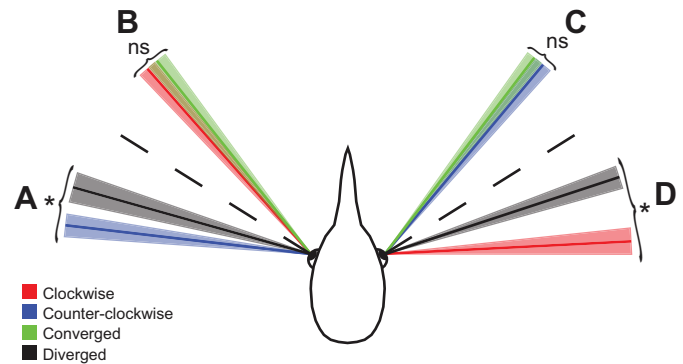
forward. Therefore, the previously measured converged states, which show a large degree of interspecific variation in the comparative visual field literature, reflect realistic values for the size of the binocular, lateral and blind areas. While starlings can also make divergent movements, they cannot achieve a state where both eyes are moved backwards to their maximum extent (Fig. 3A,D). This finding has important implications for the study of avian visual fields (e.g. Martin, 2014; Moore et al., 2015). From a functional perspective, our results mean that when birds diverge their eyes to reduce the size of their blind areas in order to increase visual coverage, the visual fields may not be as wide as previously reported in the literature. Actual diverged states would fall somewhere between the measured diverged state and the measured at-rest state. This leads to two hypothetical scenarios depending on whether the constraints in eye divergence are species specific or not. If eye divergence is limited similarly across all species, then previous comparative relationships involving diverged visual fields should remain unchanged. Alternatively, if species differ in the ability to fully diverge their eyes, then previous hypotheses about the visual coverage increase or binocular field reduction may be questioned (e.g. Moore et al., 2013).

Taking into account our results and previous results (Bloch et al., 1984; Voss and Bischof, 2009; Wallman and Pettigrew, 1985; Wallman et al., 1994), it is apparent that there is large diversity in avian oculomotor strategies. Interspecific variation in oculomotor

strategies suggests that saccades may be specialized for the specific ecological conditions that each species faces. However, there may be inherent trade-offs in oculomotor strategies. For example, we might expect generalist foragers or species in complex visual habitats (e.g. closed habitats) to use a more plastic oculomotor strategy to deal with the large amount of uncertainty about where and how visual challenges will present themselves. Conversely, specialist foragers or species in visually simple habitats (e.g. open habitats) may use a constrained oculomotor strategy because the type and location of visual challenges are more predictable. To fully understand the ultimate selective pressures involved in shaping oculomotor strategies, more comparative information is necessary in animals whose ecological conditions differ.

MATERIALS AND METHODS

Subjects were 12 adult (at least second year) European starlings (seven males, five females) caught from wild populations in Tippecanoe County, IN, USA (N 40.4417, W 86.9300). We housed the birds indoors in black wire cages (0.6×0.6×0.75 m) on a 14 h:10 h light:dark cycle. Birds were kept in visual and auditory contact with conspecifics. We provided the birds with water, cat food and game bird maintenance chow *ad libitum*. The Purdue University Institutional Animal Care and Use Committee approved all procedures (protocol 111200398).

To characterize the oculomotor strategy of European starlings, we used an eye-tracking system designed for small birds with laterally placed eyes (following Tyrrell et al., 2014). We restrained the heads and bodies of subjects following the approach of previous spontaneous eye saccade studies to create repeatable conditions that facilitate comparisons between species and between studies (Voss and Bischof, 2009; Wallman and Pettigrew, 1985). The experimental arena consisted of a central platform, which housed the subject bird and the eye-tracker apparatus, surrounded by three display screens (Fig. 4A). The subject's body was restrained in a custom-designed foam cradle wrapped with soft Velcro straps and the beak was held in a wire bracket to stabilize the head. The three display screens surrounding the central platform were positioned 74 cm away from the center of the subject's head. The forward display screen was aligned perpendicular to the subject's beak axis, and the two side screens were aligned 70 deg inward from the plane of the front screen (Fig. 4A). For this experiment, the display screens remained solid gray, and spontaneous saccades were recorded for 30 s.

The eye-tracking system consisted of two small infrared-sensitive cameras directed towards the subject's eyes (hereafter eye cameras) to monitor changes in the position of the eyes, and two small infrared-sensitive cameras directed towards the two lateral display screens (hereafter scene cameras) to record the scene viewed by the subject. The scene cameras were positioned above the subject's head, and eye cameras were positioned slightly caudal with respect to the subject's optic axis to avoid blocking foveal gaze. The video feeds from all four cameras were synchronized and multiplexed into a single video file using an H.264 converter box (Blackmagic H.264 Pro Recorder, Melbourne, Australia) and recorded on a DVR (LOREX Vantage ECO2, Baltimore, MD, USA).

PSBinocularTracker software (Positive Science LLC, New York, NY, USA) was used to track the dark pupil centroid and the corneal reflection centroid (Fig. 4B), the latter of which was generated by an infrared-LED that was mounted to the side of each eye camera. Each individual video trial was calibrated using the behavioral calibration technique presented in Tyrrell et al. (2014), which allowed PSBinocularTracker to superimpose the subject's foveal gaze onto the display screens (Fig. 4B). The position of foveal gaze is preferable to raw eye position because raw eye position is highly sensitive to noise generated by small head movements, whereas gaze position takes into account the relationship between the pupil center and the corneal reflection to provide a reliable output despite small head movements. Furthermore, saccade magnitude can be interpreted angularly with gaze position, which compensates for the 3D rotational nature of a nearly spherical eye, whereas raw eye position presents 2D linear movements.
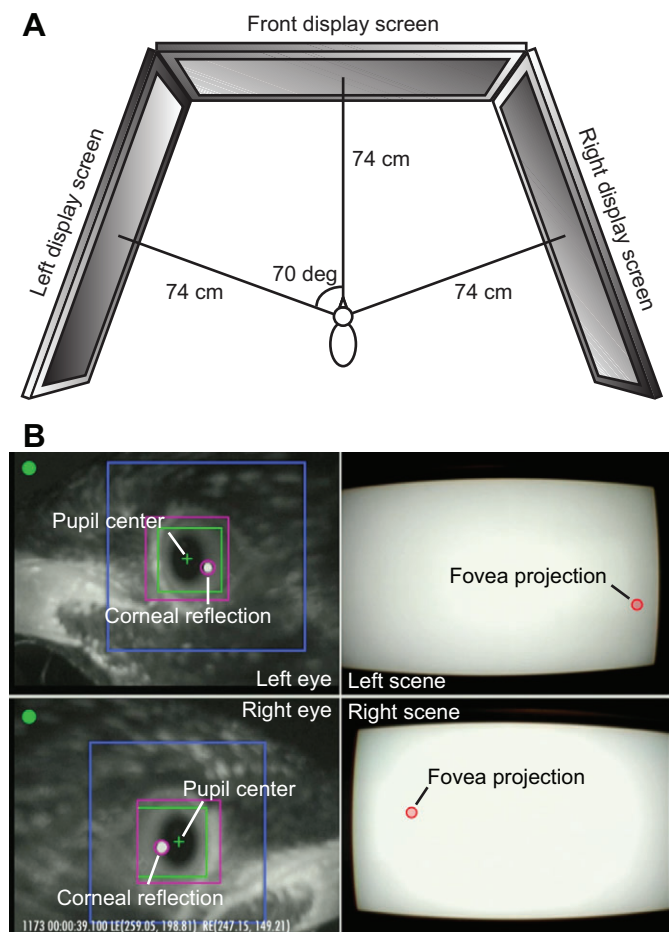

Fig. 4. Experimental procedure. (A) Schematic diagram of the experimental arena. (B) Example frame from video output indicating the ocular landmarks that are tracked and the resulting location of the foveal gaze.

PSBinocularTracker generates a file that contains Cartesian coordinate values for gaze position at each video frame (30 frames s^{-1}). Data from frames where the subject's eye was closed or obscured by the nictitating membrane were excluded because the pupil could not be tracked. One of the observers (S.R.B.) identified the frames corresponding to the beginning and end of a saccade by scrubbing through the video files frame by frame, after verifying 95% consistency with another observer (L.P.T.).

To determine the primary saccade axis in starlings, we first needed to establish that eye movements did indeed follow an axial distribution. Therefore, we tested eye movement patterns for reflective symmetry (symmetry about two axes) using the 'circular' package for circular statistics in R (version 3.1.0) following Pewsey et al. (2013). We tested each eye separately (two eyes each from 12 individuals) and found that 22 of the 24 eyes showed reflective symmetry. This led us to conclude that the eye movements were axial and should be treated as diametrically bimodal data. There is no established method for dealing with repeated measures designs in circular statistics. Therefore, we avoided pseudoreplication by calculating the mean saccade axis for each eye. Then, we calculated each individual starling's mean axis by averaging the mean value of the left eye with the mean value of the right eye. We calculated the primary saccade axis from the remaining 12 data points (one for each individual), allowing us to run circular statistics without violating the independence assumption. We present mean resultant length ($\bar{R}$) as the measure of variation for circular data. $\bar{R}$-values range from 0 to 1, with 0 indicating a uniform distribution and values close to 1 indicating tightly clustered data. We also determined whether the angle of the axis differed between the eyes using Moore's test for paired circular data (Pewsey et al., 2013).

Furthermore, we divided the direction of saccades into four quadrants: dorso-nasal, ventro-nasal, ventro-temporal and dorso-temporal. We used the direction of gaze change to assign quadrants, unless gaze angle and pupil angle were on opposite sides of a quadrant boundary and within <15 deg of the quadrant boundary. For these exceptions (<5% of saccades), we averaged gaze and pupil angle to increase the robustness of the categorization. We calculated the rate and magnitude of saccades within each quadrant using a general linear mixed model repeated on eye nested within individual and sex as a covariate. Saccade rate (s^{-1}) was the dependent variable for one analysis and amplitude for the other analysis. We used Tukey–Kramer pairwise comparisons to determine significance levels between treatment levels. We log transformed the amplitude of saccades, as its residuals were not normally distributed.

We also asked whether the angle of the primary gaze position axis differed when the eye was moved in front of or behind its resting position, as is the case with pigeons (Bloch et al., 1984; Lemeignan et al., 1992). We found the resting position on the horizontal axis of each eye for each individual using a Loess regression in R. Then, we separated eye movements that started in front of or behind the horizontal resting position (defined by the peak of the Loess regression). We then determined the mean eye movement axes using the 'circular' package in R. Movements originating in front of the resting position were compared with movements made behind the resting position using Moore's test for paired circular data (Pewsey et al., 2013).

Given the presence of a primary gaze axis for spontaneous saccades, we also tested whether starlings were able to fixate on stimuli presented off the primary axis of movement. We showed them video clips of a moving mealworm, a stimulus that starlings generally fixate on (Tyrrell et al., 2014). Mealworms were concentrated in two locations: the dorso-nasal region of the display screen (off the saccade axis) or the ventro-nasal region of the display screen (on the saccade axis). Fixations on the mealworm were defined as a fixation during the 4 s stimulus presentation and within 5 deg of the stimulus. The probabilities of fixating on mealworms in the two locations were compared using a general linear mixed model repeating on individual and eye.

To determine whether starling saccades were independent (i.e. the left and right eye act independently of one another) or conjugate (i.e. the left and right eye are yoked in time and amplitude of movement), we calculated the relative saccade amplitude by dividing the smaller eye amplitude by the larger eye amplitude for each eye saccade. Relative saccade amplitude yields a unitless value between 0 and 1, with values close to 0 indicating one eye

moved much further than the other, and values close to 1 indicating the two eyes moved a similar distance. We first asked whether the distribution of relative saccade amplitudes differed from a random, uniform distribution using a Kolmogorov–Smirnov test. For each bird, we calculated the proportion of saccades that fell into 20 different categories of relative saccade amplitude (i.e. we binned in increments of 0.05). After verifying that this distribution was significantly different from random, we asked in which direction it differed using a general linear mixed model. We binned the relative saccade amplitude into categories of 0.25 (following Voss and Bischof, 2009) and calculated the proportion of saccades that fell into each category for each individual.

To determine whether starlings were limited in their ability to converge or diverge their eyes, we defined four states that represent the different combinations of maximum forward and backward eye positions that could be achieved by moving both eyes. First, in the converged state, both eyes moved forward (see green areas in Fig. 3). Second, in the diverged state, both eyes moved backward (see black areas in Fig. 3). Third, in the clockwise state, the left eye moved forward but the right eye moved backward (see red areas in Fig. 3). Fourth, in the counter-clockwise state, the left eye moved backward but the right eye moved forward (see blue areas in Fig. 3). The video frame in which the cumulative forward or backward positions of the left and right eyes were the greatest was defined as the maximum eye position. We used maximum eye position for each individual rather than average eye position because the goal was to determine whether starlings could physically attain the maximum eye position in convergent or divergent states.

If starlings can fully converge their eyes, then the positions between the converged state of the left eye versus the clockwise state of the left eye (Fig. 3B) as well as the converged state of the right eye versus the counter-clockwise state of the right eye (Fig. 3C) would not be significantly different. If starlings can fully diverge their eyes, then the positions between the diverged state of the left eye versus the counter-clockwise state of the left eye (Fig. 3A) as well as the diverged state of the right eye versus the clockwise state of the right eye (Fig. 3D) would not be significantly different. Eye positions were compared using paired t-tests. We also compared the rate at which starlings made saccades in the same direction (converge or diverge) with the rate of saccades in opposite directions (clockwise or counter-clockwise) using a paired t-test. All statistical analyses were run in SAS 9.3. We present means±s.e. throughout.

Author contributions
All authors contributed to the experiment design and prepared the manuscript; L.P.T. and S.R.B. performed the experiments and analyses.

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