



Great-tailed grackles can independently direct their eyes toward different targets

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Abstract

Many species use eye movements to direct their overt attention toward specific targets within their environments. Some species can move each eye independently but we have a limited understanding of whether they can simultaneously monitor different targets with each eye. This study, therefore, tested whether a songbird can independently move its eyes towards two different targets. Captive great-tailed grackles (*Quiscalus mexicanus*) were simultaneously presented with one target in their left visual field and another target in their right visual field; the targets were both in the upper visual fields, both in the lower visual fields, or one target was in the upper visual field of one eye, while the other target was in the lower visual field of the other eye. The grackles correctly directed their left and right eyes toward the targets regardless of where the targets appeared at levels greater than chance. These results demonstrate that an avian species can perform simultaneous eye movements towards two different targets.

Keywords Bird · Eye movements · Eye coordination · Eye tracking · Independent eye movements · Lateral eyes · Monocular · Sensory · Oculomotor control

Introduction

Species often use eye movements to quickly direct their overt attention toward specific targets within their environments (Land 1999, 2015; Hayhoe and Ballard 2005; Yorzinski et al. 2013). Individuals in some species, such as birds and lizards, can move each eye independently (Bloch et al. 1984; Wallman and Pettigrew 1985; Tyrrell et al. 2015; Katz et al. 2015; Yorzinski 2019). In some cases, the two eyes can be coordinated through central mechanisms (Wallman and Letelier 1993). For example, when pigeons (*Carneau rouge*) eat or peahens (*Pavo cristatus*) jump, both of their eyes converge to the food or landing spot, respectively, even when one of the eyes is covered (Bloch et al. 1984; Yorzinski 2019). In other cases, the two eyes are not coordinated and each eye moves in directions unrelated to the other eye. In pigeons, their left and right eyes move in uncoordinated

directions when stimuli appear in their lateral visual fields (Bloch et al. 1984). When individuals exhibit independent eye movements, it is possible for them to direct one eye towards one target while directing their other eye toward another target (Bloch et al. 1984).

Relatively few studies have examined whether animals can move their eyes independently to direct their overt attention toward two targets. One study found that common chameleons (*Chamaeleo chamaeleon*) are able to do so by tracking two targets that are moving in opposite directions (Katz et al. 2015). In contrast, another study found that zebra finches (*Taeniopygia guttata*) are unable to simultaneously direct their eyes toward two targets: when one of their eyes moves toward a target, the other eye performs a counter movement in the opposite direction (Voss and Bischof 2009). We have a limited understanding of whether other species that can move their eyes independently can simultaneously monitor two different targets.

This study, therefore, tested the hypothesis that an avian species can independently move its eyes towards two different targets. It tested this hypothesis using captive great-tailed grackles (*Quiscalus mexicanus*), a common songbird species with laterally placed eyes (Johnson and Peer 2001). The grackles were simultaneously shown one target in their

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left visual field and another target in their right visual field, while their eye movements were recorded. The targets were both in the upper visual fields, both in the lower visual fields, or one was in the upper visual field, while the other was in the lower visual field. The targets consisted of images of human faces; because songbirds perceive humans as threats (Carter et al. 2008), the faces were expected to evoke strong visual orienting responses. It was predicted that the grackles would move their left eyes toward the targets in the left visual field and their right eyes towards the targets in the right visual field, regardless of whether the targets appeared in the upper or lower visual fields.

Methods

The eye movements of captive female great-tailed grackles (*Quiscalus mexicanus*; $n = 32$) were examined between April 2019 and April 2020. Adult females were captured from the wild in College Station, Texas and the surrounding area and then housed in outdoor aviaries (2.1 m \times 2.1 m \times 1.9 m; 30.56° N, 96.41° W). Only females were tested because of logistical difficulties in capturing males from the wild. They were given food and water ad libitum. The study was approved by Texas A&M University's Animal Care and Use Committee (#2019-0219).

For each trial, a bird was individually transported from its outdoor aviary to an indoor cage (0.76 \times 0.46 \times 0.46 m). The bird remained within this cage for at least 30 min so that it could acclimate to being indoors (food and water were provided ad libitum). After this acclimation period, the bird was secured in a foam cradle using velcro straps and placed in the middle of the testing arena. The testing arena consisted of a section (0.83 m \times 0.61 m \times 0.66 m) within a large plastic box that contained two monitors (Dell 27" S2716DG; 144 Hz; 2560 \times 1440 pixels) positioned on each side of the cradle (Fig. 1a). A LED light strip on the roof of the testing arena provided lighting (2.2 kLux). The bill of the bird was fastened to a wooden dowel that was secured to the middle of the testing arena floor to keep the bird's head positioned at a constant angle relative to the monitors. Three video cameras (Canon VIXIA HF R70; 60 frames/s) recorded the testing arena: two video cameras were located on opposite sides of the bird to record each eye and a third video camera was placed behind the bird to record one of the monitors.

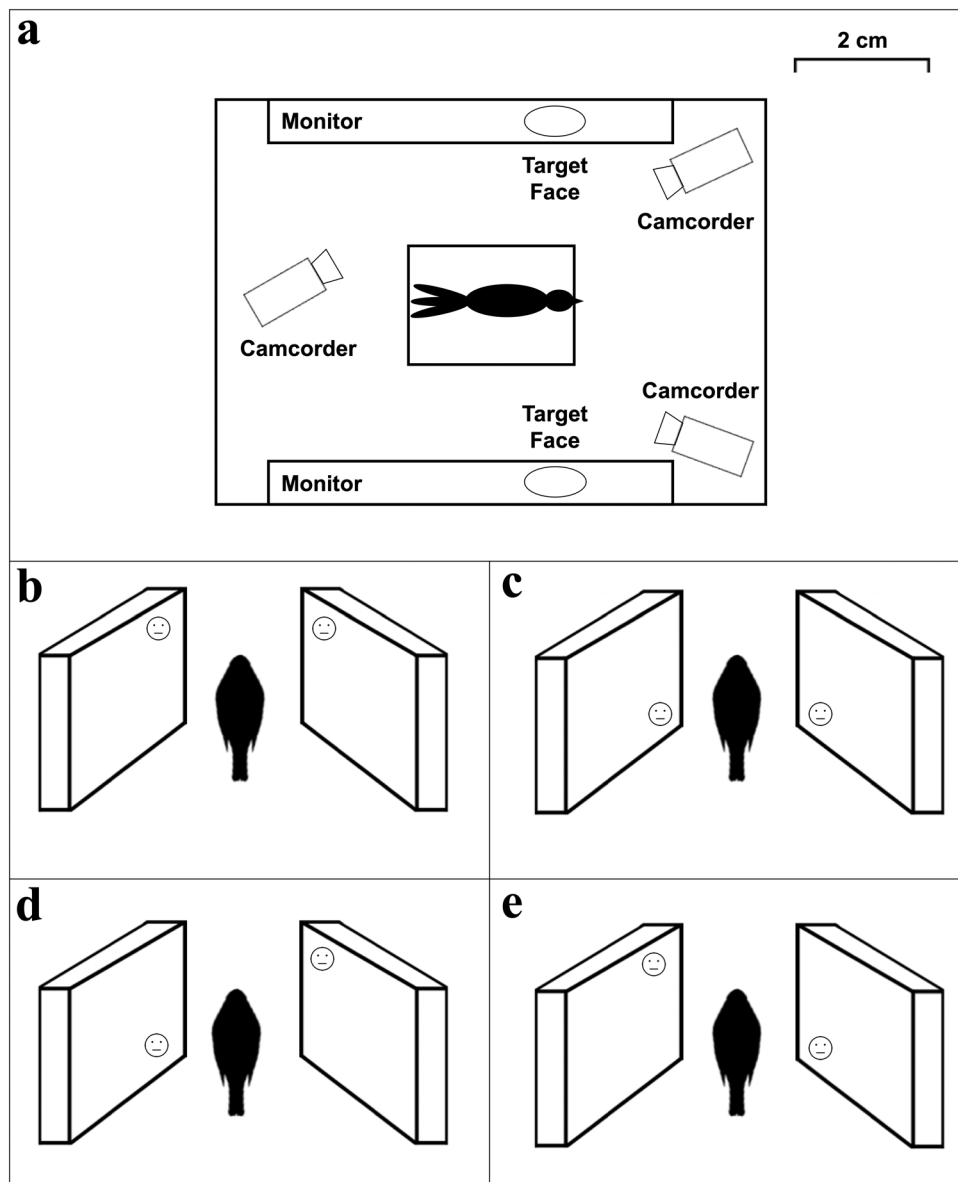
Each bird was exposed to two simultaneously presented stationary targets (one target presented in the left visual field and one target presented in the right visual field) in four different stimulus configurations. The first pair of targets appeared five minutes after the bird was secured in the foam cradle to allow time for the bird to adjust to the testing arena, and it appeared for ten seconds. The pair of targets was displayed for ten seconds to provide a brief exposure while

minimizing habituation. 5 min elapsed before the next pair of targets appeared (this was done to minimize order effects), and the pair of targets was also displayed for ten seconds; this process was repeated until the pairs of targets from each configuration were presented. A white background was displayed on both monitors between the presentation of targets. The targets consisted of human face images. The human faces simulated a person at approximately 0.62 m away (targets were 0.093 m height \times 0.093 m width; subtending 20° height \times 20° width), exhibited neutral expressions, depicted women, and their eyes and faces were oriented straight ahead (Langner et al. 2010). The faces were positioned atop a white background that filled the screen and the faces were matched for luminance.

The four different stimulus configurations consisted of (1) both targets appearing in the upper visual fields (LURU; Fig. 1b), (2) both targets appearing in the lower visual fields (LDRD; Fig. 1c), (3) one target appearing in the lower visual field of the left eye and one target appearing in the upper visual field of the right eye (LDRU; Fig. 1d), and (4) one target appearing in the upper visual field of the left eye and one target appearing in the lower visual field of the right eye (LURD; Fig. 1e). The angle between the middle of the birds' orbits and the middle of the targets that were located in the upper or lower visual fields was approximately 28° up or down, respectively, along the vertical axis. All of the targets were located in the same position along the horizontal axis such that they were perpendicular to the birds' orbits (Fig. 1a). The presentation order of the targets from each stimulus configuration was pseudorandomized across birds such that targets from each stimulus configuration appeared an equal number of times in each order (for example, one-quarter of the birds saw targets in the LURU configuration first). Ten different target faces were used across birds and a given bird never saw the same target face twice. A bird was exposed to targets from the four stimulus configurations one time each to minimize habituation to the face stimuli (D'earth and Dawkins 1996). As such, a given bird saw four pairs of targets, one each of the LURU, LDRD, LDRU, and LURD configurations. Overall, 32 birds were tested. Custom Matlab scripts were used to present the targets.

All of the videos from a given trial were synchronized. The eye movement immediately preceding each target's appearance and the first eye movement following each target's appearance were located and the frames at which they began and ended were extracted as image files. The start of the second eye movement after the target appeared defined the end of the fixation period associated with the first eye movement after the target appeared. Eye movements between the left and right eye were classified as synchronized if they began moving within 2 frames of each other. The images were then rotated, if needed, so that they were correctly oriented relative to the display

Fig. 1 a Experimental setup from a top-down view (drawn to scale). Location of the targets when **b** the targets are both in the upper visual fields (LURU), **c** the targets are both in the lower visual fields (LDRD), **d** one target is in the lower visual field of the left eye and one target is in the upper visual field of the right eye (LDRU), and **e** one target is in the upper visual field of the left eye and one target is in the lower visual field of the right eye (LURD). The monitors are angled outwards for illustration purposes only (**b–e** not to scale); they were perpendicular to the birds' eyes in the experiment as depicted in **a**



monitors. Next, the images were imported into ImageJ (version 2.0) and the x - y coordinates of the pupil centers were determined. The x - y coordinates of the pupil center before and after each eye movement were used to generate polar coordinates. The polar coordinates, therefore, represent the direction that the eye moved relative to the position of the eye immediately before each eye movement. Relative to this eye position immediately preceding each eye movement, a bird could move its eye toward the front of the monitor and upwards (vector falls between 0° and 90°), toward the back of the monitor and upwards (vector falls between 90° and 180°), toward the back of the monitor and downwards (vector falls between 180° and 270°), or toward the front of the monitor and downwards (vector falls between 270° and 360°).

The targets likely fell within the peripheral visual field of the grackles. The targets appeared 28° above or below the grackles' eyes in the vertical axis and 90° from the grackles' beaks in the horizontal axis. In other passerine species, the area centralis does not project more than 13° upwards or downwards, and it does not project more than 65° from the beak when the birds are at rest (Moore et al. 2015). Assuming the grackles had their eyes directed at random locations immediately before the targets appeared, the birds would need to move their eyes backwards along the horizontal axis and either upwards or downwards along the vertical axis to best resolve these peripheral targets once they appeared. A correct response was scored when the bird simultaneously moved both eyes toward the target. For example, if one target was in the upper visual field of the left eye and the other

target was in the lower visual field of the right eye, a correct response was scored when both of the bird's eyes moved backwards along the horizontal axis but the left eye moved upwards and right eye moved downwards.

The data were analyzed using circular statistics (Berens 2009; Agostinelli and Lund 2013) and binomial proportions (PROC FREQ; Version 9.4; SAS Institute Inc., Cary, NC). Rayleigh tests were performed to test whether the direction of eye movements was uniformly distributed or not (Fisher 1995). In cases when the data did not meet the underlying assumptions of the Rayleigh test (assessed using the Watson's goodness of fit test for the von Mises distribution), the omnibus test was used instead. The mean resultant vector, angular standard deviation, and resultant vector length were calculated (resultant vector lengths closer to one indicate that the data are more closely concentrated around the mean). Because the birds' precise gaze positions relative to the targets were not measured, only the direction (not the amplitude) of their eye movements was analyzed.

Binomial proportions tested whether the appearance of the targets elicited eye movements in directions that were consistent with the animals directing their gaze toward the targets (assuming the animals were directing their gaze toward random locations immediately before the targets appeared). Because the left and right eye could move independently along the horizontal and vertical axes, the chance level was set to 6.25% (there are 16 possible combinations of left and right eye movements along the horizontal and vertical axis when eyes move at the same time). The birds rarely moved one of their eyes, while their other eye remained in the same position (see "Results"). Before the targets became visible, four separate binomial proportions tests were performed to examine whether the birds moved their eyes backwards along the horizontal axis and both of their eyes upwards, both of their eyes downwards, the left eye upwards and the right eye downwards, or the left eye downwards and

the right eye upwards along the vertical axis at levels different from chance (1 eye movement preceding each stimulus configuration \times 4 stimulus configurations \times 32 birds = 128 eye movements). These four tests were performed, because they included the eye movement patterns that would be necessary to correctly orient toward the targets. After the targets became visible, four separate binomial proportions tests were performed to examine whether the birds moved their eyes in the correct directions relative to the targets (1 eye movement following each stimulus configuration \times 4 stimulus configurations \times 32 birds = 128 eye movements). Lastly, a repeated-measures generalized linear mixed model (PROC GLIMMIX; binary distribution) was performed to examine the accuracy of their eye movements relative to the four stimulus configurations, their latency to first move their eyes after the targets appeared, and the duration of the fixations after they first moved their eyes once the targets appeared. Raw *p* values are reported.

Results

Before and after the targets appeared, the birds most often (98% of the time) moved their left and right eyes at the same time. In the remainder of the eye movements (2%), the birds moved one of their eyes but the other eye remained in the same position. The birds usually (85.9% of the time) moved their eyes within 0.5 s of the targets' initial appearance.

Before the targets appeared, the birds moved their left and right eyes in random directions ($p > 0.05$; Table 1; Fig. 2). Compared to chance (6.25%), the birds were equally likely to move both eyes backwards and upwards (4.7%; $n = 128$, $Z = 0.73$, $p = 0.47$), both eyes backwards and downwards (3.1%; $n = 128$; $Z = 1.46$, $p = 0.14$), both eyes backward but the left eye downwards and the right eye upwards (3.9%; $n = 128$, $Z = 1.10$, $p = 0.27$), or both

Table 1 Mean resultant vector (degrees) and angular standard deviation (SD), resultant vector length, and uniformity test statistic (and raw *p* value) for the left and right eye movements before and after the targets appeared

Target	Eye	Vector mean (SD)		Vector length		Uniformity Statistic (<i>p</i> value)	
		Before	After	Before	After	Before	After
LURU	Left	59 (1.2)	120 (1.1)	0.24	0.37	9 (0.18) [†]	4.46 (0.011)*
	Right	175 (1.4)	122 (1.2)	0.02	0.33	0.011 (0.99)	3.50 (0.03)*
LDRD	Left	345 (1.3)	238 (1.1)	0.10	0.34	0.31 (0.74)	3.69 (0.024)*
	Right	70 (1.2)	254 (0.8)	0.24	0.64	1.79 (0.17)	13.08 (<0.0001)*
LDRU	Left	262 (1.3)	235 (1.0)	0.16	0.49	0.83 (0.44)	7.76 (0.0003)*
	Right	153 (1.3)	112 (1.1)	0.11	0.35	0.36 (0.70)	7 (0.028)* [†]
LURD	Left	253 (1.2)	123 (0.7)	0.30	0.79	2.96 (0.050)	0 (<0.0001)* [†]
	Right	73 (1.3)	253 (0.9)	0.16	0.62	0.85 (0.43)	12.11 (<0.0001)*

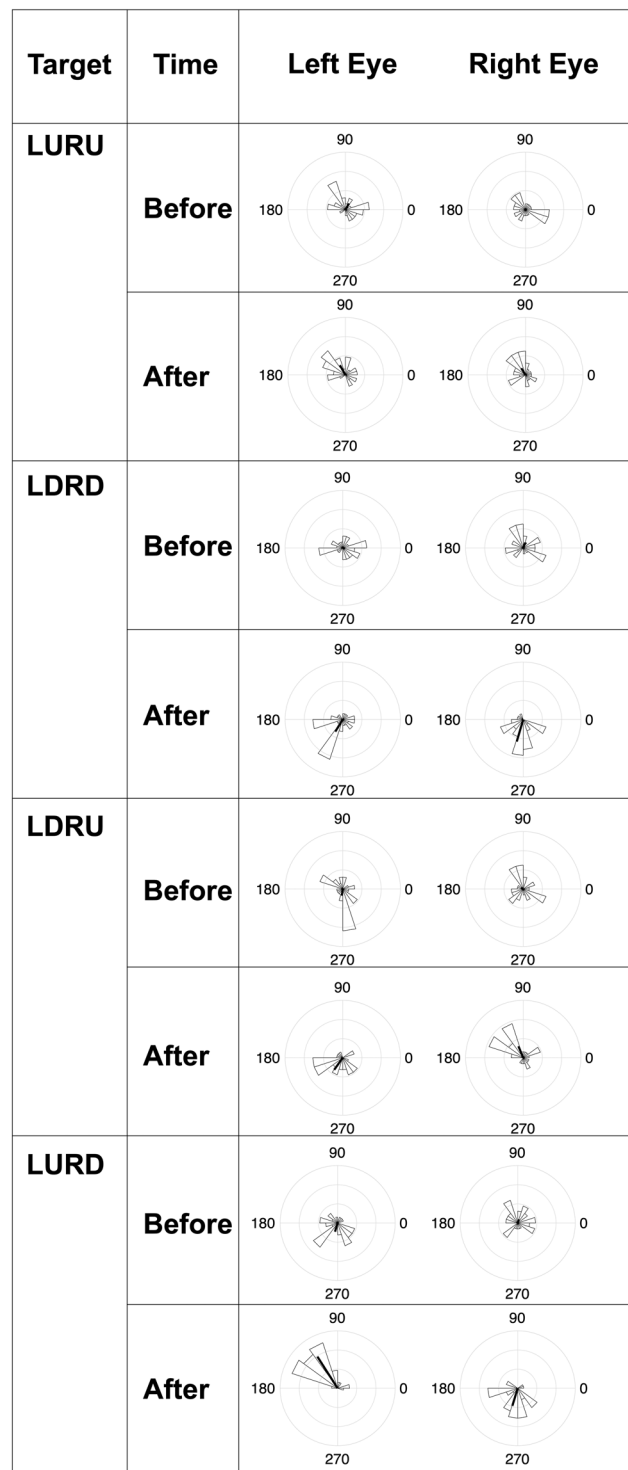
The uniformity test was the Rayleigh test except in cases when the data did not meet the underlying assumptions; in those cases, the omnibus test was performed instead (indicated with a †). The uniformity statistic is the z-statistic for the Rayleigh tests and *m* value (minimum number of samples falling in one half of the circle) for the omnibus tests. Asterisks indicate statistically significant results

Fig. 2 Circular diagrams displaying eye movements of the left and right eyes before and after targets appeared in the (1) upper visual fields (LURU), (2) lower visual fields (LDRD), (3) lower visual field of the left eye and upper visual field of the right eye (LDRU), and (4) upper visual field of the left eye and lower visual field of the right eye (LURD) in 20 degree wedges. Each diagram displays eye movements from the 32 birds. The radial axis value is 0.1 for the inner most circle, 0.2 for the middle circle, and 0.3 for the outmost circle. The thick line represents the direction and magnitude of the mean resultant vector. 0°–180° = horizontal axis (0° is towards the front of the monitor and 180° is towards the back of the monitor), 90°–270° = vertical axis (90° is upwards and 270° is downwards).

eyes backwards but the left eye upwards and the right eye downwards (3.1%; $n = 115$, $Z = 1.46$, $p = 0.14$) before the targets were visible (Fig. 3a).

After the targets appeared, the birds moved their left and right eyes in non-random directions ($p < 0.05$; Table 1; Fig. 2; Online Resource 1). They directed their eyes toward the targets regardless of where the targets appeared within the visual fields. Compared to chance (6.25%), the birds were more likely to move both of their eyes toward the targets when the targets were in the upper visual field of both eyes (18.75% correct; $n = 32$, $Z = 2.92$, $p = 0.0035$), lower visual field of both eyes (28.13% correct; $n = 32$, $Z = 5.11$, $p < 0.0001$), lower visual field of the left eye and upper visual field of the right eye (21.88% correct; $n = 32$, $Z = 3.65$, $p = 0.0003$), or upper visual field of the left eye and lower visual field of the right eye (37.50% correct; $n = 32$, $Z = 7.30$, $p < 0.0001$; Fig. 3b).

The grackles were more likely to move their eyes toward the correct targets when the targets were in upper visual field of the left eye and lower visual field of the right eye compared with when the targets were in the upper visual fields of both eyes ($t = 2.49$, $df = 31$, $p = 0.018$); there were otherwise no statistically significant differences in how accurately the grackles moved their eyes toward the targets among stimulus configurations ($p > 0.05$). The grackles were quicker to move their eyes after the targets appeared when they did so in the correct directions relative to the targets rather than the incorrect directions (mean \pm SE: 0.31 ± 0.03 s (correct), 0.59 ± 0.09 s (incorrect); $F_{1,31} = 15.05$, $p = 0.0005$). The duration of their fixations that immediately followed their eye movements once the targets appeared was unrelated to whether they moved their eyes in the correct directions relative to the targets or not [mean \pm SE: 1.3 ± 0.4 s (correct), 0.9 ± 0.08 s (incorrect); $F_{1,31} = 0.95$, $p = 0.34$].



Discussion

These results demonstrate that great-tailed grackles can independently direct their two eyes toward different targets. When one target appeared in the upper visual field of the left eye and the other target simultaneously appeared in the lower visual field of the right eye (or vice versa), the birds

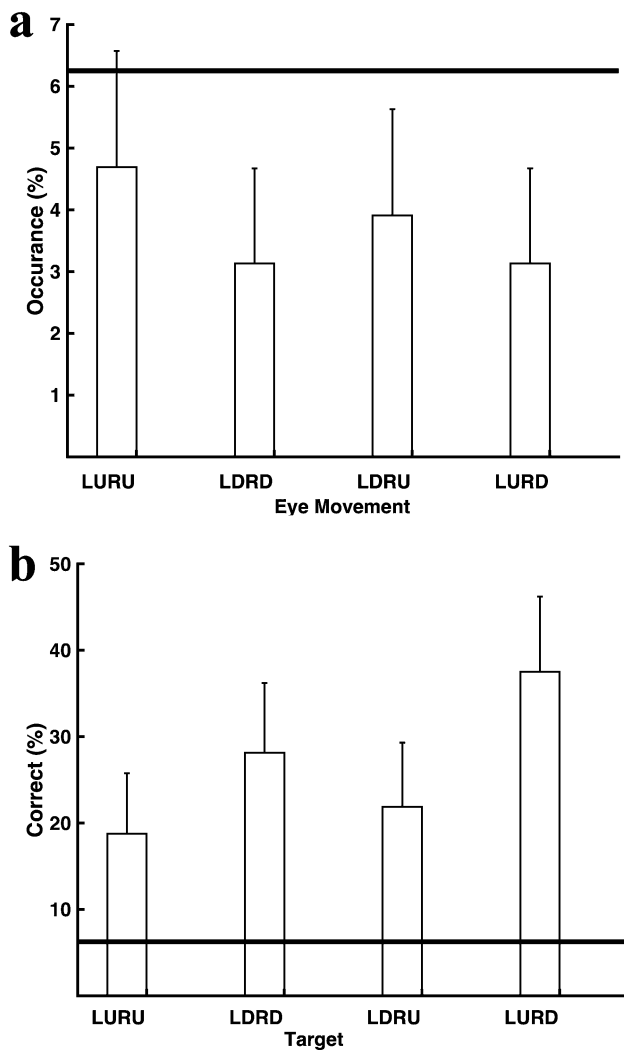


Fig. 3 **a** Percentage of eye movements immediately before the targets appeared that were directed toward the upper visual fields in both eyes (LURU), lower visual fields in both eyes (LDRD), lower visual field in the left eye and upper visual field in the right eye (LDRU), or upper visual field in the left eye and lower visual field in the right eye (LURD). **b** Percentage of correct eye movements immediately after the targets appeared in the upper visual fields (LURU), lower visual fields (LDRD), lower visual field of the left eye and upper visual field of the right eye (LDRU), or upper visual field of the left eye and lower visual field of the right eye (LURD). The horizontal lines correspond to chance expectation (6.25%)

directed each eye toward the target. Similarly, when the targets simultaneously appeared in the upper or lower visual fields of both eyes, the birds again directed their eyes toward the targets.

Many avian species can move their left and right eyes independently of each other (pigeons: Bloch et al. 1984, tawny frogmouths and little eagles: Wallman and Pettigrew 1985; European starlings: Tyrrell et al. 2015; peafowl: Yorzinski 2019). Even when they move their eyes independently of each other, they typically move both eyes at the

same time (Wallman and Pettigrew 1985; Lemeignan et al. 1992; Tyrrell et al. 2015; Yorzinski 2019). In some species, these independent eye movements can be coordinated, such as when the eyes converge to eat food (Bloch et al. 1984) or land on perches (Yorzinski 2019). When the eyes converge, the frontal binocular field (area that both eyes can simultaneously view) of many birds is often approximately 15° – 30° wide (Martin 2009). Similar to these other avian species, great-tailed grackles can also independently move their left and right eyes and they most often do so synchronously. When they were presented with lateral targets, the grackles moved their eyes toward the targets regardless of whether that required the eyes to move in the same direction or not. The tectofugal visual system is primarily responsible for processing information from both eyes in laterally eyed birds (Engelage and Bischof, 1988; Voss and Bischof, 2003), and it was, therefore, likely involved when the grackles were viewing the two targets. The optic tectum (homolog of the mammalian superior colliculus) within the tectofugal pathway is likely particularly important for controlling their eye movements (Du Lac and Knudsen 1990; Wylie et al. 2009). Given the potential role of omnipause neurons in controlling saccadic eye movements in birds (Yang et al. 2008), it is possible that these neurons are involved in synchronizing saccades between the two eyes.

By moving their eyes independently of each other, individuals can potentially direct their overt attention towards two targets simultaneously or rapidly alternate their overt attention between two targets (Roberts et al. 1996; Ott et al. 1998). Only one study has examined whether individuals that can move their eyes independently of each other are able to perform simultaneous monocular tracking. In this study, chameleons were presented with two targets moving in opposite directions, and they simultaneously tracked the targets independently in each eye (Katz et al. 2015). Similarly, the current study found that an avian species is able to independently direct each eye toward two separate targets. The great-tailed grackles moved their eyes independently toward targets (human faces) that simultaneously appeared in their left and right visual fields. Individuals that move each eye independently can potentially attend to different stimuli within their environments simultaneously, maximizing their chances of detecting and monitoring important information. The grackles' ability to independently move their eyes may be particularly beneficial when they are foraging for food on the ground while simultaneously scanning for predators in the sky (Wallman and Letelier 1993). Studies examining the eye movements of grackles when they are foraging in natural environments could provide evidence for this possible benefit. Only one other study has tested whether birds can simultaneously move their eyes towards two targets but the species studied (zebra finches) could not perform independent eye movements; as such, when one of

their eyes moved in one direction toward a target, the other eye moved in the opposite direction irrespective of the target position (Voss and Bischof 2009).

Future experiments that vary the type of targets could further advance our understanding of avian oculomotor strategies. For example, the grackles may exhibit a high probability of moving their eyes toward targets when the targets are extremely threatening (such as looming predators); conversely, they may ignore targets that are irrelevant (such as stones or other inanimate objects). When one target is highly threatening and the other is irrelevant, they may rapidly shift their eye toward the threatening target while ignoring the irrelevant target. It is important to note that the grackles were restrained in this study such that they could not move their bodies or heads: this setup was necessary to precisely monitor their eye movements relative to the targets. Additional studies in freely moving birds could highlight the significance of eye movements in natural contexts. It would be especially interesting to consider cases in which birds are locomoting and the eye movements employed for successful locomotion (such as head bobbing; Pratt 1982; Wohlschläger et al. 1993; Cronin et al. 2005) potentially conflict with those employed for other tasks (such as monitoring a predator).

While the visual system of great-tailed grackles has not been studied, it is highly likely that the targets used in this study appeared within their peripheral visual fields. In the closely related brown-headed cowbird, their visual field is so wide that the birds can see far above and below them in the vertical plane and nearly all around them in the horizontal plane (Blackwell et al. 2009). Closely related species also have a retinal specialization that consists of a single area of high retinal ganglion cell density (Dolan and Fernández-Juricic 2010; Fernández-Juricic et al. 2019) that typically projects no more than 13° upwards or downwards in the vertical plane and 65° from the beak in the horizontal plane (Moore et al. 2015). Assuming the grackles have a visual system that is similar to these closely related species, the grackles most likely viewed the targets (appearing 28° upwards or downwards in the vertical plane and 90° from the beak in the horizontal plane) with their peripheral vision rather than a retinal specialization. Assuming the grackles were not directing their eyes at their extreme limits when the targets appeared (Wallman and Pettigrew 1985), the grackles would need to make eye movements toward the peripheral targets to maximize resolution. Future studies could track the exact gaze position of birds (Yorzinski et al. 2013) to determine whether they can simultaneously fixate targets within each visual field rather than only moving their eyes closer to those targets (as demonstrated in this study). Furthermore, additional studies could examine whether the initial position of the eyes influences subsequent eye movements towards targets; it is possible that the grackles were already directing their eyes close to the targets when they appeared and

they would, therefore, gain little additional information by moving their eyes even closer to the targets. In humans and macaques, for example, gaze shifts are influenced by the initial eye position (Harris 1995; McCluskey and Cullen 2007). Overall, the grackles did move their eyes toward the targets (despite likely variability in the initial position of their eyes relative to the targets) but this effect may have been stronger if initial eye movement positions were accounted for.

Birds with laterally placed eyes continuously receive visual information to both eyes and must integrate this information to inform their behavioral decisions (Remy and Watanabe 1993). This study demonstrated that an avian species can perform simultaneous eye movements with the left and right eyes moving toward different targets in their lateral visual fields. Future studies are needed to examine how simultaneous information to each eye is processed and used to make decisions (Roberts et al. 1996). In some cases, information from one eye may be ignored when information from the other eye is more relevant (Palmer and Zeier 1974).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00221-021-06122-8>.

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Author contributions JLY conceived the study, analyzed the data and wrote the manuscript.

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Data availability All data generated or analyzed during this study are included in this published article (and its supplementary information files: Online Resource 1 & 2).

Declarations

Conflict of interest The author declares no conflicts of interest.

Ethical approval All experiments complied with the laws of the United States and international ethical standards. This study was approved by Texas A&M University's Institutional Animal Care and Use Committee (no. 2019-0219), Texas Parks and Wildlife Department (SPR-1116-279), United States Fish and Wildlife Service (MB160637-0 and MB47977D-0) and United States Geological Survey Bird Banding Laboratory (24067).

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