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RESEARCH ARTICLE

Conjugate eye movements guide jumping locomotion in an avian species

Jessica L. Yorzinski

ABSTRACT

Many animals rely on vision to successfully locomote through their environments. However, our understanding of the interaction between vision and locomotion is surprisingly limited. This study therefore examined the visual mechanisms guiding jumping locomotion in an avian species. It recorded the eye movements of captive Indian peafowl (*Pavo cristatus*) as they jumped up onto and down from a perch. Peafowl shifted their eyes forward as they were jumping, increasing the degree of binocular overlap. Their eye movements were highly conjugate as they were jumping but were otherwise loosely conjugate. Finally, the peafowl rarely directed their gaze toward landing spots. These results suggest that eye movements play a central role in avian locomotion and they can vary depending on the specific locomotor task.

KEY WORDS: Attention, Binocular vision, Laterally placed eyes, Lateral vision, Binocular overlap, Peafowl

INTRODUCTION

Many animals rely heavily on vision during locomotion. Individuals can actively move their eyes to direct their attention toward relevant objects along their locomotor trajectory (Patla and Vickers, 1997; Land et al., 1999; Franchak and Adolph, 2010). They can learn about the size, composition and location of these objects to inform their locomotor decisions (Patla, 1997). However, we know little about how animals use vision to guide locomotion (Matthis et al., 2018). In humans (*Homo sapiens*), individuals rarely fixate terrain when walking over terrain that is simple (such as a paved walkway), presumably because their peripheral vision is sufficient to detect any impediments in the relatively predictable path (Pelz and Rothkopf, 2007). In contrast, when walking over complex terrain (such as boulders), adults often fixate several steps ahead of them because high visual acuity is likely needed on such unpredictable paths to avoid missteps (Matthis et al., 2018). This work in humans suggests that overt attention (attending to targets with fixations) and covert attention (attending to targets without fixations; peripheral vision; Posner, 1980) play central roles in locomotion that vary depending on the specific locomotor task.

Aside from work in humans, we know little about how other animals use attention to guide their locomotion. In one of the few studies examining attention and locomotion in non-human animals, it was found that domestic cats (*Felis catus*) look ahead of them (instead of looking at their feet) when walking over terrain of varying complexity, suggesting that they use overt attention for planning their future steps rather than executing their current one; in addition, the cats spend more time looking at the terrain when the terrain is complex (Rivers et al., 2014). Because non-human animals vary widely in their visual systems (Martin, 2007), the mechanisms guiding locomotion could differ dramatically across species (Dunlap and Mowrer, 1931). In animals with laterally placed eyes, the axes of their eyes' optics often project approximately perpendicular to the direction of movement. As such, it is possible that they use their binocular field – the frontal visual field simultaneously viewed by both eyes – during locomotion (Martin, 2009), but this has never been empirically tested.

The aim of this study was therefore to investigate the visual mechanisms guiding locomotion in a species with laterally placed eyes, focusing on jumping locomotion. Indian peafowl (*Pavo cristatus*) are an appropriate species with laterally placed eyes to examine this topic because their primary forms of locomotion are walking on the ground and jumping (Parveen et al., 2018). This study investigated the eye movements of female peafowl when they engaged in jumping locomotion. Furthermore, it examined where female peafowl directed their gaze when jumping. Their gaze was defined as the projection of their area centralis, an area of high retinal ganglion cell density with the highest visual acuity that is similar to the human fovea (Hart, 2002).

MATERIALS AND METHODS

I examined the eye movements of 24 adult female peafowl, *Pavo cristatus* Linnaeus 1758 ('peahens'), between May 2017 and March 2018 in College Station, TX, USA (30.56°N, 96.41°W). The birds were housed in an outdoor enclosure (18.3 m×24.4 m×2.1 m) and given food and water *ad libitum*. They were captured as adults from feral populations in Florida and California at least 4 years prior to the start of this study. The study was approved by Texas A&M University's Animal Care and Use Committee (#2016-0216).

For each trial, a bird was outfitted with a telemetric, binocular eye-tracker (Fig. 1A; Positive Science, LLC, New York, NY, USA; headpiece: 33 g; backpack: 317 g). The eye-tracker had two cameras that recorded each eye of the bird and another two cameras that recorded the scene in front of each eye (specifications of each camera: 30 frames s^{-1}; 320×240 pixels; 113×85 mm). The scene cameras were positioned such that they were roughly centered along the primary gaze position of each eye (they were each directed approximately 55 deg horizontally from the beak; Fig. 1); given the field of view of each scene camera (100 deg×77 deg), the scene cameras did not completely cover the entire frontal visual field (it was not necessary, however, for the cameras to completely cover the entire frontal visual field because the peahens' gaze did not extend directly in front of their beaks). The eye-tracker was calibrated using an oculometric approach based on corneal reflections (Fantz, 1958; Hamada, 1984; Yorzinski et al., 2013). This calibration procedure is highly accurate (<5 deg of error;

Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, USA.

*Author for correspondence (jyorzinski@tamu.edu)

J.L.Y., 0000-0002-4193-6695

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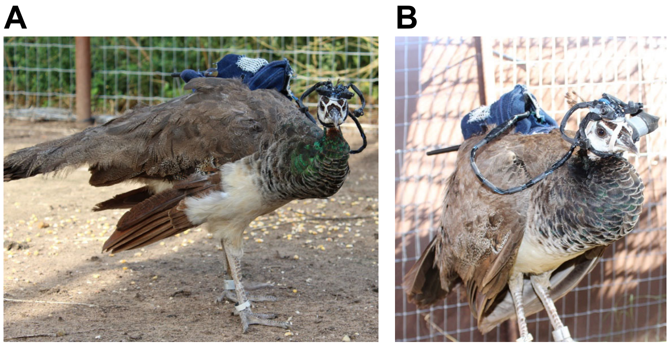

Fig. 1. Peahens wearing the eye-tracker. A peahen wearing the eye-tracker without the patch (A) and with the patch covering her left eye (B).

Yorzinski et al., 2013) and tracks the area centralis (an area of high retinal ganglion cell density with the highest visual acuity that is similar to the human fovea) of the peahens (Hart, 2002).

The bird was then released into a pre-experimental room (6.1 m×6.1 m×2.1 m) that was within the main enclosure but was separated from the rest of the enclosure by plywood boards so that the bird could not see the rest of the flock; the bird remained in this room for 5 min in order to adjust to wearing the eye-tracker. After this adjustment period, I entered the pre-experimental room and walked behind the bird until she moved into the adjacent, experimental room (24.4 m×6.1 m×2.1 m), which was also separated from the rest of the enclosure by plywood boards. The experimental room contained obstacles (17 cinderblocks; 0.2 m×0.2 m×0.4 m each) as well as a wooden perch (0.8 m high and 0.4 m wide) at the far end of the room. It also contained four camcorders (Swann SWPRO 535CAM security cameras; Swann Security Systems, Santa Fe Springs, CA, USA) multiplexed to a DVR (4-channel HD DVR; Night Owl Security Products LLC, Naples, FL, USA) that recorded the experimental room and were synchronized with the eye-tracker videos. I continued to walk behind the bird until she jumped atop the perch. After 2 min, I approached the bird so that she would jump off the perch. I then walked behind the bird until she reached the opposite side of the room, and removed her from the experimental room.

The birds were tested on two different days that were separated by at least 7 days (mean±s.e.m.: 72.5±10.3 days). The birds' eyes were completely uncovered on one day (Fig. 1A) but had a patch over one eye on the other day (Fig. 1B). When there was a patch over one eye, the eye movements of that eye were still recorded by the eye-tracker because the eye-tracker camera was enclosed within the patch. Half of the birds had a patch on their left eye while the other half of the birds had a patch on their right eye. The order of days (both eyes uncovered versus one eye uncovered) was randomized across birds. Only one bird could not be tested on both days because of health concerns: she was therefore tested on one day with her right eye uncovered and her left eye covered.

From each trial, video clips before, during and after the bird jumped up onto or down from the perch were isolated. The before clip consisted of the 5 s immediately before the bird jumped up onto

Table 1. The effect of jump type, eye open, behavior and their interactions on the standardized *X*–*Y* positions of the pupil centers

		X-axis: *F*-value (*P*-value)		*Y*-axis: *F*-value (*P*-value)	
Overall model	d.f. num., den.	Left eye	Right eye	Left eye	Right eye
Jump type	1, 23	119.2 (<0.0001)*	23.5 (<0.0001)*	4.25 (0.051)	3.72 (0.066)
Eye open	2, 23	4.65 (0.02)*	81.8 (<0.0001)*	6.14 (0.0073)*	12.78 (0.0002)*
Behavior	2, 23	298.46 (<0.0001)*	76.31 (<0.0001)*	4.93 (0.017)*	8.04 (0.0023)*
Jump type × eye open	2, 23	0.19 (0.83)	0.03 (0.97)	0.32 (0.73)	3.22 (0.058)
Jump type × behavior	2, 23	20.99 (<0.0001)*	21.61 (<0.0001)*	70.97 (<0.0001)*	80.91 (<0.0001)*
Eye open × behavior	4, 23	9.63 (0.0001)*	9.34 (0.0001)*	2.15 (0.11)	8.6 (0.0002)*
Jump type × eye open×behavior	4, 23	4.56 (0.0074)*	1.46 (0.25)	2.16 (0.11)	4.8 (0.0058)*
Comparisons					
Both eyes uncovered: up					
Before vs during	1, 23	12.64 (<0.0001)*	11.37 (<0.0001)*	5.26 (<0.0001)*	4.28 (0.0003)*
Before vs after	1, 23	3.68 (0.0013)*	1.4 (0.18)	6.16 (<0.0001)*	8.08 (<0.0001)*
During vs after	1, 23	18.97 (<0.0001)*	9.69 (<0.0001)*	2.68 (0.0134)*	4.26 (0.0003)*
Both eyes uncovered: down					
Before vs during	1, 23	15.6 (<0.0001)*	3.45 (0.0022)*	7.6 (<0.0001)*	3.91 (0.0007)*
Before vs after	1, 23	0.41 (0.68)	0.25 (0.81)	5.51 (<0.0001)*	1.62 (0.12)
During vs after	1, 23	12.05 (<0.0001)*	3.3 (0.0031)*	1.6 (0.12)	1.23 (0.23)
Left eye uncovered: up					
Before vs during	1, 23	9.41 (<0.0001)*	2.96 (0.007)*	1.7 (0.10)	2.06 (0.051)
Before vs after	1, 23	1.12 (0.27)	0.69 (0.49)	3.4 (0.0025)*	5.34 (<0.0001)*
During vs after	1, 23	11.08 (<0.0001)*	3.61 (0.0015)*	2.76 (0.011)*	3.35 (0.0028)*
Left eye uncovered: down					
Before vs during	1, 23	5.31 (<0.0001)*	0.2 (0.84)	4.1 (0.0004)*	4.74 (<0.0001)*
Before vs after	1, 23	3.89 (0.0007)*	1.38 (0.18)	2.35 (0.028)*	4.61 (0.0001)*
During vs after	1, 23	8.72 (<0.0001)*	1.8 (0.084)	1.56 (0.13)	1.16 (0.26)
Right eye uncovered: up					
Before vs during	1, 23	8.26 (<0.0001)*	8.1 (<0.0001)*	5.73 (<0.0001)*	2.09 (0.048)
Before vs after	1, 23	1.38 (0.18)	2.1 (0.047)	5.42 (<0.0001)*	5.12 (<0.0001)*
During vs after	1, 23	10 (<0.0001)*	9.91 (<0.0001)*	0.26 (0.79)	2.96 (0.007)*
Right eye uncovered: down					
Before vs during	1, 23	3.35 (0.0028)*	1.31 (0.20)	4.51 (0.0002)*	8.36 (<0.0001)*
Before vs after	1, 23	4.35 (0.0002)*	3.47 (0.0021)*	5.19 (<0.0001)*	8.23 (<0.0001)*
During vs after	1, 23	7.63 (<0.0001)*	5.18 (<0.0001)*	0.59 (0.56)	1.6 (0.12)

Asterisks indicate statistical significance.

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or down from the perch and the after clip consisted of the 5 s immediately after the bird jumped up onto or down from the perch. The bird jumped up onto the perch by stepping with one foot ('first step'), then stepping with the other foot, crouching down slightly, and pushing off the ground with both feet. The jump up to the perch started when the bird took her 'first step' and ended when the bird's feet were in contact with the perch and her wings were flush with her body. The jump down started when the bird first started moving her body or head downward and ended when the bird's feet were in contact with the ground and her wings were flush with her body. The 'during' clip consisted of the period when the bird was jumping up onto or down from the perch. While the before and after clips each lasted 5 s, the duration of the during clips varied across birds during the jump up (mean±s.e.m.: 1.3±0.07 s) and jump down (mean ±s.e.m.: 1.9±0.06 s). Using Yarbus Assisted (Positive Science, LLC, New York, NY, USA), the eye-tracker videos were processed by manually outlining the pupils during each frame of the clips. The outputted data file contained *X–Y* coordinates of the pupil centers from the eye cameras and *X–Y* coordinates of the gaze positions (based on the oculometric calibration procedure) from the scene cameras for each video frame. Only a small portion of the *X–Y* coordinates and associated *X–Y* gaze coordinates (2.9% in the before clips, 1.4% in the during clips and 10% in the after clips) could not be analyzed as a result of sun glare, poor transmission or the birds closing their eyes.

The *X–Y* coordinates of the pupil centers were standardized to relative *X–Y* coordinates. The *X–Y* coordinates of the pupil centers in pixels were first converted into millimeters (the width of the peahen eye is approximately 10 mm). Next, these *X* and *Y* coordinates of the pupil centers in millimeters were standardized by dividing them by the maximum *X* and *Y* coordinates, respectively, within each jump up or down clip of each bird. An *X* coordinate of 1 indicated that the bird's eye was positioned closest to the beak while a value <1 indicated that the bird's eye was more lateral; similarly, a *Y* coordinate of 1 indicated that the bird's eye was positioned furthest upward while a value <1 indicated that the bird's eye was more downward.

The *X–Y* coordinates of the gaze positions were adjusted for parallax errors (Maurer, 1975; Yorzinski et al., 2013). Parallax errors exist because the scene camera cannot be perfectly aligned with the eye of the bird without physically blocking the bird's vision. The scene camera was approximately 30 mm above the eye and either 15 mm to the right of the eye (when recording from the left eye) or 15 mm to the left of the eye (when recording from the right eye). Because the exact target of the bird's gaze was unknown, the gaze was conservatively adjusted assuming that the target was 1 m away (this approximate target distance is similar to that used in other studies examining locomotion using eye tracking; Franchak and Adolph, 2010). The videos were analyzed frame-by-frame to determine where the birds were directing their gaze. In the jump-up clips, the target was the perch; in the jump-down clips, the target was the landing spot. Because of errors associated with the eye-tracker (Yorzinski et al., 2013) and errors associated with estimating parallax errors (Maurer, 1975), I conservatively created a 10 deg radius around each point of gaze. For each gaze coordinate, I determined whether the target fell within this 10 deg radius. The percentage of time that the birds spent looking at the targets before and during the jump up or down was calculated (when both eyes were uncovered, the mean time of the left and right eyes was calculated; when only one eye was uncovered, the time of the uncovered eye was calculated).

The standardized *X–Y* coordinates of the pupil centers were compared using repeated-measures mixed linear models in SAS (PROC MIXED; version 9.4; SAS Institute Inc., Cary, NC, USA). The mean of the standardized *X–Y* coordinates of the pupil centers for each behavior (before, during and after the jump up or down) for each bird were used in the analyses. The dependent variables were the standardized *X* coordinate of the left eye, *X* coordinate of the right eye, *Y* coordinate of the left eye, or *Y* coordinate of the right eye. The independent variables were the jump type (up or down), eye open (both eyes uncovered, left eye uncovered or right eye uncovered), behavior (before, during or after the jump up or down) and their interactions. The independence of the left and right eyes

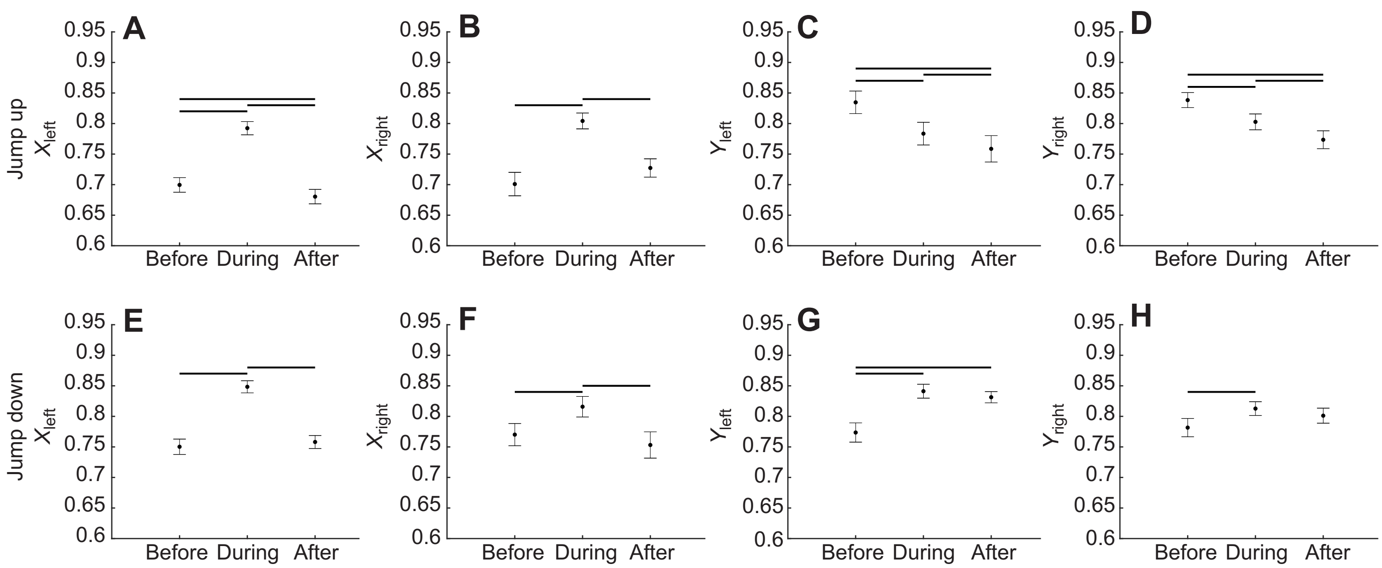

Fig. 2. Eye positions when both eyes were uncovered. Eye positions are shown before, during and after the peahens (*n*=23) jumped up onto a perch (A: *X*-axis of left eye; B: *X*-axis of right eye; C: *Y*-axis of left eye; D: *Y*-axis of right eye) or down from a perch (E: *X*-axis of left eye; F: *X*-axis of right eye; G: *Y*-axis of left eye; H: *Y*-axis of right eye). An *X*-axis value of 1 indicates that the bird's eye is positioned closest to the beak while a value <1 indicates that the bird's eye is more lateral; similarly, a *Y*-axis value of 1 indicates that the bird's eye is positioned furthest upward while a value <1 indicates that the bird's eye is more downward. Means±s.e.m. are displayed; horizontal lines indicate statistically significant comparisons.

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was also compared using repeated-measures generalized linear models. The dependent variable was the correlation coefficient (the correlation coefficients between the left and right eye of each bird for each jump type, eye open, behavior and eye direction was used). The independent variables were the jump type, eye open, behavior, eye direction (eye movement along the *X*- or *Y*-axis) and their interactions. *A priori* predictions were made regarding differences among independent variables and contrasts were created to evaluate these differences; the false discovery rate correction was used to evaluate statistical significance (Benjamini and Hochberg, 1995).

To confirm that the eye-tracker was not influencing jumping behavior, the head orientation of peahens (n=10) as they jumped onto the perch was video recorded from above (240 frames s^{-1}; Hero 5; GoPro, Inc., San Mateo, CA, USA) when the birds were not wearing the eye-tracker. During every 10th frame of each jump, the coordinates of the beak tip, middle of the head and middle of the body (between the scapulae) were measured (ImageJ software; http://rsbweb.nih.gov/ij/). The angle between the head position (a line connecting the beak tip and middle of the head) and body position (a line connecting the middle of the head and middle of the body) was measured (Fig. S1). When the head position and body position were aligned (the bill, head and body fell along a straight line), the angle was zero.

RESULTS

Peahens shifted their eyes forward along the *X*-axis (horizontal axis) when jumping up onto and down from the perch (Table 1, Figs 2 and 3; Movie 1). Even when one of their eyes was covered, the covered eye still shifted forward along the *X*-axis when the birds jumped up onto the perch; the covered eye also shifted forward when the birds jumped down from the perch but only when the left eye was covered (Table 1, Figs 4 and 5).

Peahens positioned their eyes upward along the *Y*-axis (vertical axis) before jumping up onto the perch (Table 1, Figs 2 and 3; Movie 1). When one eye was covered, the covered eye also was positioned upward along the *Y*-axis before the peahens jumped up onto the perch (Table 1, Figs 4 and 5). Before jumping down from the perch, the peahens positioned their left eyes downward along the *Y*-axis and their right eyes exhibited a similar trend (Table 1, Figs 2 and 3). When one eye was covered, the covered eye was also

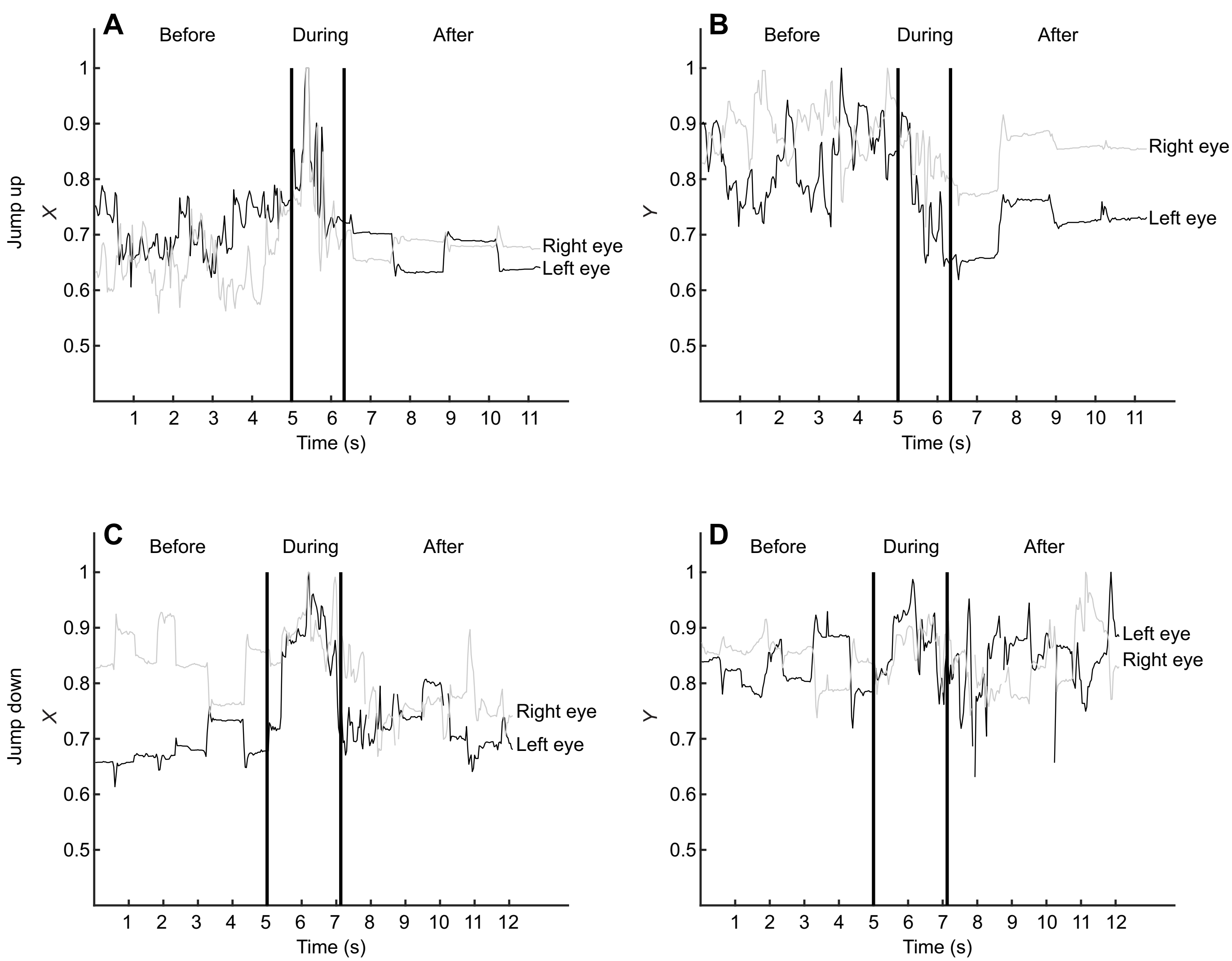

Fig. 3. Exemplar eye positions when both eyes were uncovered. Example time series of the eye positions of a peahen before, during and after she jumped up onto (A: *X*-axis; B: *Y*-axis) or down from (C: *X*-axis; D: *Y*-axis) a perch. An *X*-axis value of 1 indicates that the bird's eye is positioned closest to the beak while a value <1 indicates that the bird's eye is more lateral; similarly, a *Y*-axis value of 1 indicates that the bird's eye is positioned furthest upward while a value <1 indicates that the bird's eye is more downward.

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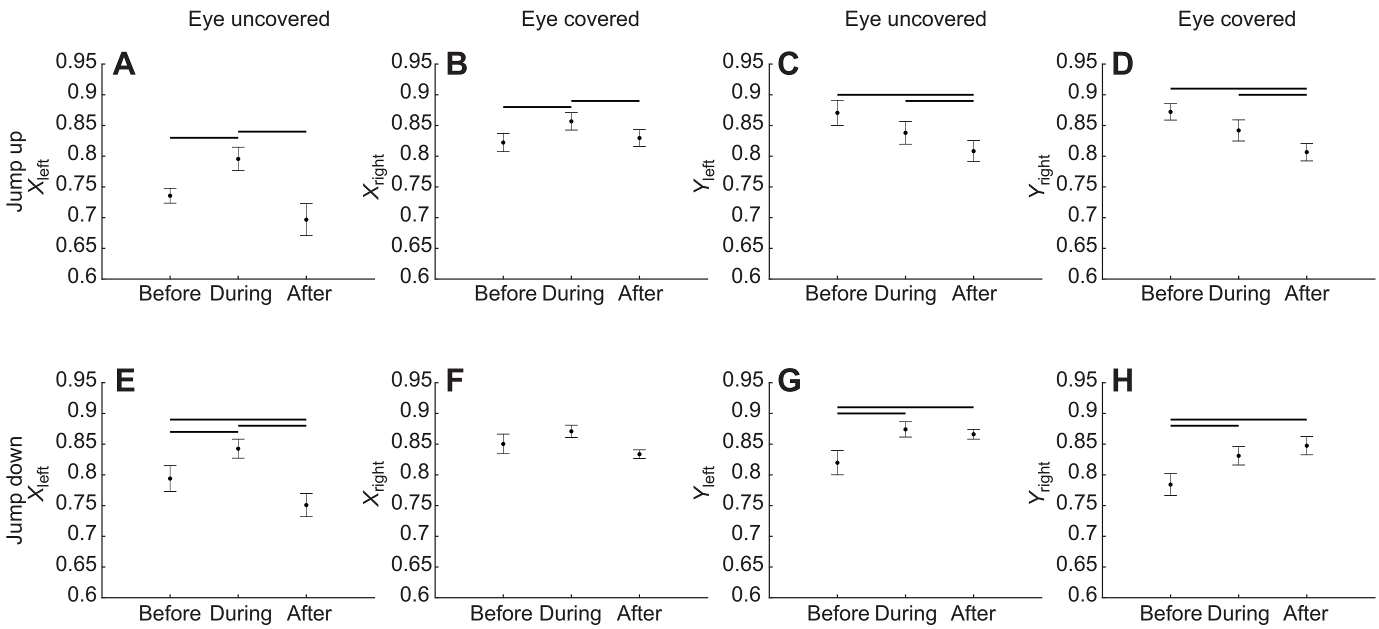

Fig. 4. Eye positions when the left eye was uncovered and the right eye was covered. Eye positions are shown before, during and after the peahens (n=12) jumped up onto a perch (A: X-axis of left eye; B: X-axis of right eye; C: Y-axis of left eye; D: Y-axis of right eye) or down from a perch (E: X-axis of left eye; F: X-axis of right eye; G: Y-axis of left eye; H: Y-axis of right eye). An X-axis value of 1 indicates that the bird's eye is positioned closest to the beak while a value <1 indicates that the bird's eye is more lateral; similarly, a Y-axis value of 1 indicates that the bird's eye is positioned furthest upward while a value <1 indicates that the bird's eye is more downward. Means±s.e.m. are displayed; horizontal lines indicate statistically significant comparisons.

positioned downward along the Y-axis before the descent (Table 1, Figs 4 and 5).

The degree of independence between the eyes varied depending on the peahens' locomotor behavior. In most cases, the left and right eyes moved independently but were generally correlated (Table 2, Fig. 6). However, the eyes were highly conjugate along the X- and Y-axis when the peahens were jumping up onto the perch, even when one eye was covered. Similarly, the eyes were highly conjugate along the X-axis, but not the Y-axis, when the peahens were jumping down from the perch, even when one eye was covered.

The peahens spent less than 15% of their time fixating the landing spots with their area centralis in the 5 s period before they jumped up onto or down from the perch (Table 3). In fact, many of the birds

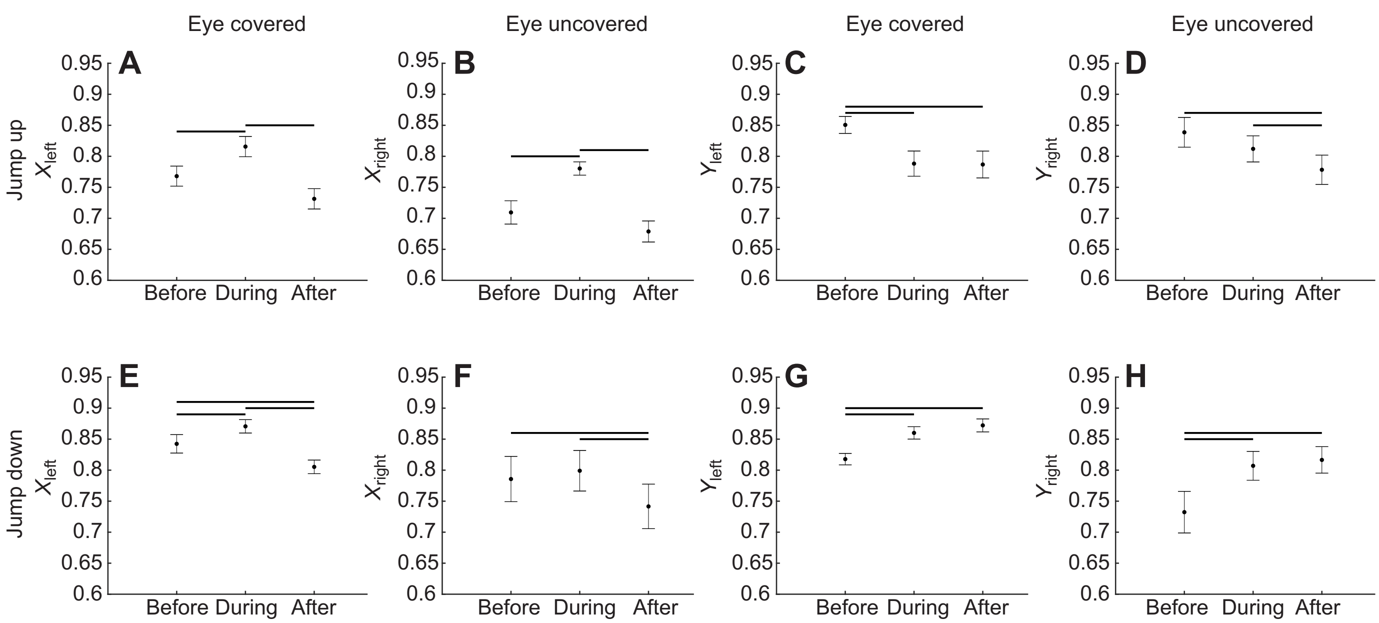

Fig. 5. Eye positions when the right eye was uncovered and the left eye was covered. Eye positions are shown before, during and after the peahens (n=12) jumped up onto a perch (A: X-axis of left eye; B: X-axis of right eye; C: Y-axis of left eye; D: Y-axis of right eye) or down from a perch (E: X-axis of left eye; F: X-axis of right eye; G: Y-axis of left eye; H: Y-axis of right eye). An X-axis value of 1 indicates that the bird's eye is positioned closest to the beak while a value <1 indicates that the bird's eye is more lateral; similarly, a Y-axis value of 1 indicates that the bird's eye is positioned furthest upward while a value <1 indicates that the bird's eye is more downward. Means±s.e.m. are displayed; horizontal lines indicate statistically significant comparisons.

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Table 2. The effect of jump type, eye open, behavior, eye direction and their interactions on the correlation coefficients between the left and right eyes.

Overall model	d.f. num., den	Correlation coefficient *F*-value (*P*-value)
Jump type	1, 23	62.94 (<0.0001)*
Eye open	2, 21	7.3 (0.0039)*
Behavior	2, 46	103.56 (<0.0001)*
Eye direction	1, 23	70.71 (<0.0001)*
Jump type × eye open	2, 21	4.33 (0.027)*
Jump type × behavior	2, 46	16.03 (<0.0001)*
Jump type × eye direction	1, 23	0.01 (0.92)
Eye open × behavior	4, 42	2.27 (0.078)
Eye open × eye direction	2, 21	14.58 (0.0001)*
Behavior × eye direction	2, 46	9.84 (0.0003)*
Jump type × eye open × behavior	4, 41	1.01 (0.41)
Jump type × eye open × eye direction	2, 21	0.95 (0.4)
Jump type × behavior × eye direction	2, 46	35.91 (<0.0001)*
Eye open × behavior × eye direction	4, 42	2.34 (0.071)
Jump type × eye open × behavior × eye direction	4, 41	0.84 (0.51)
Comparisons		
Both eyes uncovered: up *X*		
Before vs during	1, 41	4.62 (<0.0001)*
Before vs after	1, 41	3.72 (0.0006)*
During vs after	1, 41	8.34 (<0.0001)*
Both eyes uncovered: up *Y*		
Before vs during	1, 41	8.46 (<0.0001)*
Before vs after	1, 41	2.43 (0.019)*
During vs after	1, 41	6.02 (<0.0001)*
Both eyes uncovered: down *X*		
Before vs during	1, 41	4.77 (<0.0001)*
Before vs after	1, 41	2.25 (0.03)*
During vs after	1, 41	2.52 (0.016)*
Both eyes uncovered: down *Y*		
Before vs during	1, 41	1.15 (0.26)
Before vs after	1, 41	2.11 (0.041)
During vs after	1, 41	3.26 (0.0022)*
Left eye uncovered: up *X*		
Before vs during	1, 41	3.03 (0.0042)*
Before vs after	1, 41	3.99 (0.0003)*
During vs after	1, 41	6.96 (<0.0001)*
Left eye uncovered: up *Y*		
Before vs during	1, 41	4.62 (<0.0001)*
Before vs after	1, 41	1.52 (0.14)
During vs after	1, 41	3 (0.0046)*
Left eye uncovered: down *X*		
Before vs during	1, 41	2.86 (0.0066)*
Before vs after	1, 41	0.41 (0.68)
During vs after	1, 41	2.45 (0.019)*
Left eye uncovered: down *Y*		
Before vs during	1, 41	2.11 (0.041)
Before vs after	1, 41	3.37 (0.0016)*
During vs after	1, 41	1.26 (0.21)
Right eye uncovered: up *X*		
Before vs during	1, 41	6.54 (<0.0001)*
Before vs after	1, 41	8.58 (<0.0001)*
During vs after	1, 41	8.58 (<0.0001)*
Right eye uncovered: up *Y*		
Before vs during	1, 41	3.38 (0.0016)*
Before vs after	1, 41	1.66 (0.1)
During vs after	1, 41	1.72 (0.094)
Right eye uncovered: down *X*		
Before vs during	1, 41	3.12 (0.0033)*
Before vs after	1, 41	0.11 (0.92)
During vs after	1, 41	3.23 (0.0025)*
Right eye uncovered: down *Y*		
Before vs during	1, 41	0.84 (0.4)
Before vs after	1, 41	1.8 (0.079)
During vs after	1, 41	2.65 (0.011)*

Asterisks indicate statistical significance.

never fixated the landing spots within these 5 s periods before they jumped up or jumped down (when both their eyes were uncovered, 17% and 70% of the birds never fixated the landing spots 5 s before they jumped up or down, respectively). The peahens' gaze never fell directly on the landing spot (perch) when the birds were jumping up. Aside from one bird, the birds' gaze never fell directly on the landing spot while the birds were jumping down; the one bird that fixated the landing spot during the descent exhibited an unusual descent in that the beak was initially directed away from the landing spot (in all other cases, the beak was pointed toward the landing spot during the jump down). When jumping up onto the perch while not wearing the eye-tracker, the peahens' heads were roughly aligned with their bodies (mean±s.e.m. offset between head and body: 11.9±2.0 deg; range: 4–27 deg) and their bodies moved perpendicularly toward the perch (Movie 2). While the angle between the peahens' heads and bodies was not measured when they were wearing the eye-tracker and jumping up onto the perch, their heads and bodies were also roughly aligned (based on the videos from the camcorders recording the experimental room).

DISCUSSION

These results demonstrate that eye movements in peafowl vary when the birds are jumping. In particular, peahens shifted their eyes forward when jumping up onto and down from a perch. Furthermore, their eye movements were highly conjugate when jumping up onto and down from a perch but were otherwise loosely conjugate. Even when one eye was covered, these eye movement patterns were largely upheld. These results are consistent with previous work in other species showing that the independence of eye movements can be task dependent (Bloch et al., 1984; Fritsches and Marshall, 2002; Katz et al., 2015; Daly et al., 2017). For example, mantis shrimp (*Odontodactylus scyllarus*) exhibit highly conjugate eye movements when startled but loosely conjugate eye movements during gaze stabilization; furthermore, when one eye is covered, this covered eye exhibits similar eye movements to the uncovered eye in some tasks but not others (Daly et al., 2017).

Even though it has been suggested that birds use their binocular fields during locomotion (Martin, 2009), this is the first experimental evidence suggesting that they do so. Binocularity in birds, in contrast to other species, does not likely have higher order functioning that provides the perception of solidity and depth perception (Martin, 2009). Instead, binocularity appears to function in providing information regarding the direction of travel and time to contact targets in each eye independently. The contralateral projection of each eye can provide a symmetrically expanding optic flow field surrounding the bill. As such, when peahens rotate their eyes forward during jumps, they can increase the amount of optic flow-field information in each eye. Because the left and right eyes can operate independently in birds, Martin (2009) has even suggested using the term 'contralateral vision' rather than 'binocular vision' to describe avian vision in the frontal visual field.

The peahens rarely directed their gaze toward the landing spots; 5 s before the birds jumped up onto or down from the perch, they spent less than 15% of their time gazing at the landing spots. However, it is possible that the birds gazed at the landing spots more often prior to the 5 s before the jumps but these time periods were not analyzed. When the peahens were in the process of jumping up or down, they never gazed directly at the landing spots (with the exception of one bird; see Results). Based on the lateral placement of their eyes, it is not surprising that the peahens rarely gazed at the landing spots during the jumps. When jumping up, the peahens' heads were roughly aligned with their bodies and their bodies were moving perpendicularly

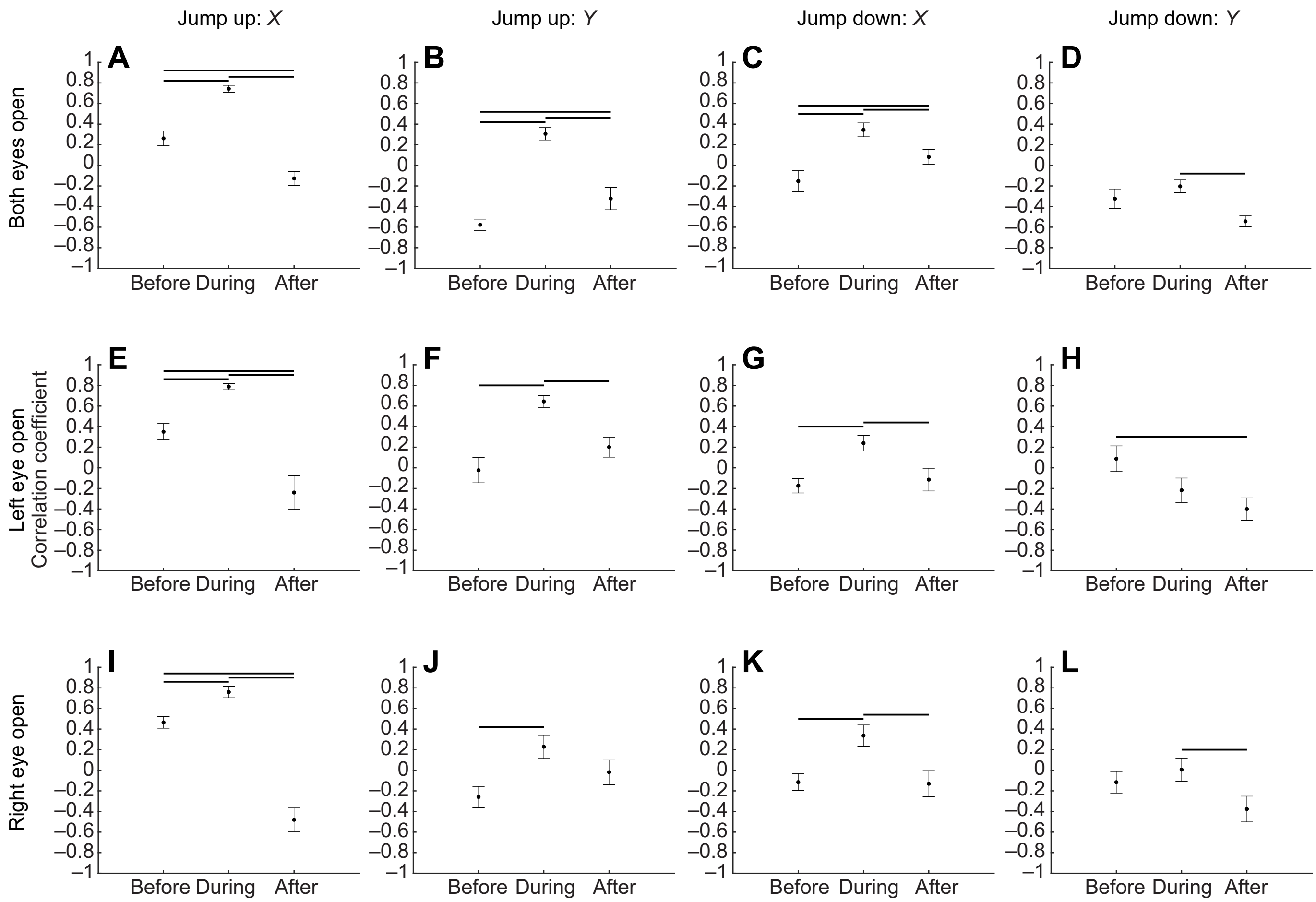

Fig. 6. Independence of eye movements. Correlation coefficients between the left and right eyes of peahens (n=24) relative to the jump type (up/down), eye open (both/left/right), behavior (before, during and after), eye direction (eye movement along the X- or Y-axis) and their interactions. Means±s.e.m. are displayed; horizontal lines indicate statistically significant comparisons.

toward the landing spots. The fovea of other birds with laterally placed eyes does not project directly in front of the birds (passerine fovea projects 46–63 deg from the beak; Moore et al., 2015). While no previous studies have determined the precise foveal projections of peafowl, their area centralis also projects laterally (as determined by the oculometric calibration procedure performed while the peahens were wearing the eye-tracker). Therefore, the peahens were likely relying on covert attention (peripheral vision; Martin, 2009) to guide their jumping locomotion as they cannot likely fixate targets with their area centralis when those targets are located directly in front of their beaks. It is possible that the birds could have gazed at the landing spots during jumps by turning their heads so that their area centralis was aligned with the landing spots even though their bodies were moving directly toward the landing spots; however, the birds were not observed engaging in this alternative strategy, potentially because their other eye would then be directed away from the landing spot. These results are remarkably similar to those found in humans. Immediately before and during jumps up, down or over obstacles, adults rarely look directly at those obstacles (Franchak and Adolph, 2010). In fact, adults fixated the obstacle only 31% of the time 5 s before jumping over them; furthermore, only 0.5% of adults fixated the obstacle during the final step of their jump (Franchak and Adolph, 2010). Future studies that investigate how gaze in non-human animals facilitates locomotion will provide valuable insight into the impressive diversity of locomotor strategies across species.

Table 3. The percentage of time that peahens spent gazing at the landing spots relative to jump type and eye open before they jumped up onto or down from the perch

	Jump up		Jump down	
	Mean± s.e.m. (%)	Range (%)	Mean± s.e.m. (%)	Range (%)
Both eyes uncovered	5.6±1.0	0–18	1.8±0.8	0–13.5
Left eye uncovered	10.8±5.3	0–52	15.4±3.5	0–41.3
Right eye uncovered	11.1±3.2	0–38	11.0±4.9	0–44.1

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Competing interests
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Data availability
Source data are available from Harvard Dataverse: https://doi.org/10.7910/DVN/JZGTXJ

Supplementary information

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References

Benjamini, Y. and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc.* **57**, 289-300. doi:10.1111/j.2517-6161.1995.tb02031.x

Bloch, S., Rivaud, S. and Martinoya, C. (1984). Comparing frontal and lateral viewing in the pigeon. III. Different patterns of eye movements for binocular and monocular fixation. *Behav. Brain Res.* **13**, 173-182. doi:10.1016/0166-4328(84)90147-5

Daly, I. M., How, M. J., Partridge, J. C. and Roberts, N. W. (2017). The independence of eye movements in a stomatopod crustacean is task dependent. *J. Exp. Biol.* **220**, 1360-1368. doi:10.1242/jeb.153692

Dunlap, K. and Mowrer, O. H. (1931). Head movements and eye functions of birds. *J. Comp. Physiol. Psychol.* **11**, 99-112. doi:10.1037/h0075905

Fantz, R. L. (1958). Pattern vision in young infants. *Psychol. Rec.* **8**, 43-47. doi:10.1007/BF03393306

Franchak, J. M. and Adolph, K. E. (2010). Visually guided navigation: head-mounted eye-tracking of natural locomotion in children and adults. *Vision Res.* **50**, 2766-2774. doi:10.1016/j.visres.2010.09.024

Fritsches, K. A. and Marshall, N. J. (2002). Independent and conjugate eye movements during optokinesis in teleost fish. *J. Exp. Biol.* **205**, 1241-1252.

Hamada, T. (1984). A method for calibrating the gain of the electro-oculogram (EOG) using the optical properties of the eye. *J. Neurosci. Methods* **10**, 259-265. doi:10.1016/0165-0270(84)90018-9

Hart, N. S. (2002). Vision in the peafowl (Aves: *Pavo cristatus*). *J. Exp. Biol.* **205**, 3925-3935.

Katz, H. K., Lustig, A., Lev-Ari, T., Nov, Y., Rivlin, E. and Katzir, G. (2015). Eye movements in chameleons are not truly independent - evidence from simultaneous monocular tracking of two targets. *J. Exp. Biol.* **218**, 2097-2105. doi:10.1242/jeb.113084

Land, M., Mennie, N. and Rusted, J. (1999). The roles of vision and eye movements in the control of activities of daily living. *Perception* **28**, 1311-1328. doi:10.1068/p2935

Martin, G. R. (2007). Visual fields and their functions in birds. *J. Ornithol.* **148**, 547-562. doi:10.1007/s10336-007-0213-6

Martin, G. R. (2009). What is binocular vision for? A birds' eye view. *J. Vision* **9**, 1-19. doi:10.1167/9.11.14

Matthis, J. S., Yates, J. L. and Hayhoe, M. M. (2018). Gaze and the control of foot placement when walking in natural terrain. *Curr. Biol.* **28**, 1224-1233. doi:10.1016/j.cub.2018.03.008

Maurer, D. (1975). Infant visual perception: methods of study. In *Infant perception: From Sensation to Cognition, Vol. 1, Basic Visual Processes* (ed. L. B. Cohen and P. Salapatek), pp. 1-76. New York, NY: Academic.

Moore, B. A., Pita, D., Tyrrell, L. P. and Fernández-Juricic, E. (2015). Vision in avian emberizid foragers: maximizing both binocular vision and fronto-lateral visual acuity. *J. Exp. Biol.* **218**, 1347-1358. doi:10.1242/jeb.108613

Parveen, Z., Sidra, S. and Khan, B. N. (2018). Diet preferences and general behavior of peafowls in captive environment. *Punjab Univ. J. Zool.* **33**, 16-21. doi:10.17582/pujz/2018.33.1.16.21

Patla, A. E. (1997). Understanding the roles of vision in the control of human locomotion. *Gait Posture* **5**, 54-69. doi:10.1016/S0966-6362(96)01109-5

Patla, A. E. and Vickers, J. N. (1997). Where and when do we look as we approach and step over an obstacle in the travel path? *Neuroreport* **8**, 3661-3665. doi:10.1097/00001756-199712010-00002

Pelz, J. B. and Rothkopf, C. (2007). Oculomotor behavior in natural and man-made. In *Eye Movements: A Window on Mind and Brain* (ed. R. P. G. van Gompel, M. H. Fischer, W. S. Murray and R. L. Hill), pp. 661-676. Oxford: Elsevier.

Posner, M. I. (1980). Orienting of attention. *Q. J Exp. Psychol.* **32**, 3-25. doi:10.1080/00335558008248231

Rivers, T. J., Sirota, M. G., Guttentag, A. I., Ogorodnikov, D. A., Shah, N. A. and Beloozerova, I. N. (2014). Gaze shifts and fixations dominate gaze behavior of walking cats. *Neuroscience* **275**, 477-499. doi:10.1016/j.neuroscience.2014.06.034

Yorzinski, J. L., Patricelli, G. L., Babcock, J. S., Pearson, J. M. and Platt, M. L. (2013). Through their eyes: selective attention in peahens during courtship. *J. Exp. Biol.* **216**, 3035-3046. doi:10.1242/jeb.087338