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RESEARCH ARTICLE

Eye and head movements shape gaze shifts in Indian peafowl

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ABSTRACT

Animals selectively direct their visual attention toward relevant aspects of their environments. They can shift their attention using a combination of eye, head and body movements. While we have a growing understanding of eye and head movements in mammals, we know little about these processes in birds. We therefore measured the eye and head movements of freely behaving Indian peafowl (*Pavo cristatus*) using a telemetric eye-tracker. Both eye and head movements contributed to gaze changes in peafowl. When gaze shifts were smaller, eye movements played a larger role than when gaze shifts were larger. The duration and velocity of eye and head movements were positively related to the size of the eye and head movements, respectively. In addition, the coordination of eye and head movements in peafowl differed from that in mammals; peafowl exhibited a near-absence of the vestibulo-ocular reflex, which may partly result from the peafowl's ability to move their heads as quickly as their eyes.

INTRODUCTION

Many animals rely on visual information to learn about their environments (Hayhoe and Ballard, 2005). To do so, they must actively direct their gaze toward relevant aspects of these environments (Dukas, 2002) using a combination of eye and head movements to control their gaze direction (Land, 2004). These eye and head movements are not necessarily linked, as eye movements can be made without any head movements and the amplitude of eye and head movements may not be the same. Small changes in gaze direction can be accomplished with eye movements but larger ones often depend on head movements (Guitton and Volle, 1987). Regardless, the eyes and head must be coordinated to ensure that gaze movements are kept short and image stabilization is maintained during fixations (Meier and Dieringer, 1993).

Such coordination has been demonstrated in mammalian visual systems. In rhesus monkeys, an individual moves its eyes and head toward a visual target. Because eye movements are faster than head movements, the eyes reach the target first. As the head continues to move toward the target, the eyes make a counter-rotation (vestibulo-ocular reflex, VOR) to compensate for the head movement and the

retinal image is therefore stabilized (Bizzi et al., 1971). Guinea pigs (Gresty, 1975), rabbits (Collewijn, 1977) and humans (Guitton and Volle, 1987) also exhibit similar coordination. The exact timing of the sequence may vary depending on the initial position of the eye (Freedman and Sparks, 1997). Aside from studies in mammals, little is known about eye–head coordination in freely moving animals.

In particular, we know little about eye–head coordination in birds. Birds exhibit a wide range of eye movements (reviewed in Land, 2015). Freely moving male Indian peafowl (*Pavo cristatus*) move their eyes about 10 deg between consecutive saccades (rapid eye movements) and have a maximum eye movement amplitude of 55 deg (Yorzinski and Platt, 2014). The saccades of unrestrained pigeons (*Columba livia*) can be as large as 26 deg (Wohlschläger et al., 1993). Birds also exhibit large head movements. Many birds, such as the Wahnes's parotia (Scholes, 2008), can move their heads up to 180 deg by changing their entire body position in a single hop. Both eye and head movements contribute to birds' overall gaze changes. In pigeons, eye movements contribute to 10–20% of gaze changes (Gioanni, 1988a).

We investigated the eye and head movements of freely moving Indian peafowl to better understand how these movements are related and coordinated in birds. Peafowl are a lekking species that are native to the Indian subcontinent. They spend most of their day on the ground (walking through dense forests and scrublands) but roost on tall structures at night (Sharma, 1969; Trivedi and Johnsingh, 1996). Many predators, such as tigers and jackals, prey upon them (Harihar et al., 2007; de Silva et al., 1996; Kannan and James, 1998). To examine how peafowl shift their gaze in naturalistic environments, we measured their eye and head movements using a telemetric eye-tracker during experiments examining selective attention (Yorzinski et al., 2013; J.L.Y., G.L.P. and M.L.P., unpublished). Because males and females may face different visual tasks, we compared the eye and head movements of males and females to determine whether the sexes differ in their gaze behavior.

MATERIALS AND METHODS

We analyzed the eye and head movements of 24 adult peafowl (*Pavo cristatus* L.; 12 females and 12 males) using a telemetric eye-tracker (Yorzinski et al., 2013; J.L.Y., G.L.P. and M.L.P., unpublished). The eye and head movements were recorded during trials in which a focal bird wearing the eye-tracker was freely moving within an outdoor testing cage (27 m perimeter). During trials in which the focal bird was a female, two adult males were in the cage with her (Yorzinski et al., 2013); during trials in which the focal bird was a male, another adult male and two adult females were in the cage with him (J.L.Y., G.L.P. and M.L.P., unpublished). We analyzed eye and head movements that occurred after the focal bird was gazing at environmental features or conspecifics. The experiments in this study were approved by Duke University (IACUC: A169-11-07).

The eye-tracker has one camera that records the eye of the bird and another camera that records the scene in front of the bird (Fig. 1). Both cameras were attached to the bird's head. From each individual bird, we randomly selected five saccades (120 total saccades; 65 recorded from the left eye and 55 recorded from the right eye). Using Yarbus Assisted (Positive Science, LLC, New York, NY, USA), we manually outlined the pupil during each frame of the saccade (it was not possible to use an automated pupil

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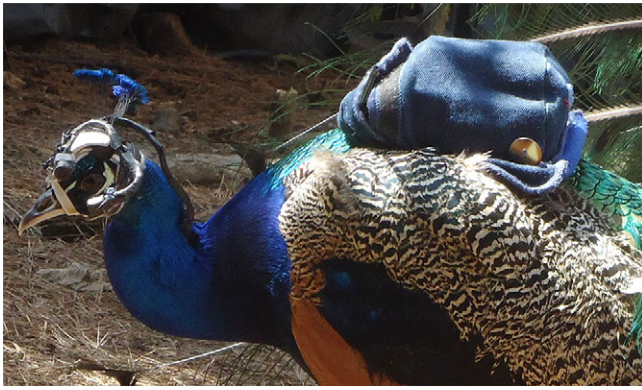*Author for correspondence (jyorzinski@purdue.edu)

Fig. 1. A peacock wearing the telemetric eye-tracker.

detection algorithm because it did not track the pupil well during saccades). We then calibrated the eye movements using an oculometric approach based on corneal reflections (Fantz, 1958; Hamada, 1984) to generate gaze coordinates overlaid on the scene camera (Yorzinski et al., 2013). We directed an LED light toward the eye of a bird and when the corneal reflection from that light was in the pupil center, the optic axis of the bird was directed toward the light and we used that eye position as a calibration point; this calibration system is very accurate with an average accuracy of about ±4 deg (Yorzinski et al., 2013). The outputted data file contained x–y coordinates of the gaze from the scene camera and the pupil center from the eye camera for each video frame. We also recorded eye movements by measuring the changing position of the edge of the iris directly from the screen image. We converted the eye movements and gaze coordinates to degrees (calibrated videos: 640 pixels horizontal×480 pixels vertical; scene camera field of view: 100 deg horizontal×77 deg vertical; eye camera field of view: 45 deg horizontal×35 deg vertical).

For each frame, we calculated the distance that the calibrated gaze point shifted on the scene camera, which moved with the bird's head ('eye-in-head movement'). We also measured the distance that the eye moved in the vertical and horizontal plane from the eye camera (this was not possible to determine from the scene camera because the scene camera orientation varied across trials). We converted these distances into millimeters relative to the actual eye size of the birds (based on a still image of a peafowl's eye as it is looking directly at a camera, the width of the eye is approximately 10 mm). Next, we determined the angular distance (in degrees) that the eye moved by using the following formula (Bloch et al., 1984):

$$\text{Eye movement} = \sin^{-1}(d/r), \qquad (1)$$

where d is the distance (mm) that the eye moved and r is the fulcrum–pupil distance (mm). The fulcrum–pupil distance is approximately 7.23 mm in peafowl {19.8 mm axial length – [3.2 mm aqueous humour pathlength+ (4.3 mm lens pathway/2)]/2; Hart, 2002}. This formula produced the distance (degrees) that the eye moved in the vertical ('vertical eye movement') and horizontal ('horizontal eye movement') direction. To verify that this calculation was accurate, we compared the angular distance that the calibrated gaze point shifted on the scene camera to the eye movement calculated based on the eye rotation. There was a high correlation between these different calculations of eye movements (Pearson correlation coefficient=0.74, $F_{1,118}$=141.74, P<0.0001).

We determined the distance that the head turned ('head movement') by recording the coordinates of a stationary object within the scene camera image (GraphClick, Arizona Software, Neuchatel, Switzerland) during each frame of a saccade and converting them to degrees. We defined the start of the saccade as when the eye-in-head movement shifted by 0.5 deg between consecutive frames and the end of the saccade when the 'eye contribution' remained within 0.5 deg between consecutive frames. Similarly, we defined the start of the head movement as when the stationary object shifted by 0.5 deg between consecutive frames, and the end of the head movement as when the stationary object remained within 0.5 deg between consecutive frames. Total gaze is the sum of the eye-in-head movement and head

movement. The eye contribution is calculated as the eye-in-head movement divided by the 'total gaze'. We performed linear mixed models (SAS, Cary, NC, USA) with repeated measures (individual bird nested within sex) and included the eye that was being recorded (left or right) as well as the sex of the bird as independent factors.

RESULTS
General
Like most other vertebrates, peafowl made high-velocity ballistic movements of both the eye and head (saccades) with clearly defined beginnings and ends (Movie 1), and with fixation intervals of varying length between them in which neither head nor eye rotated (Fig. 2). During these saccades, we did not observe instances in which the eyes rotated in the head in the absence of a head movement, although for smaller gaze changes the contribution of the eye movement often exceeded that of the head. Peafowl make oblique and even vertical eye and head movements, but most head turns are horizontal or nearly so.

Contributions of head and eye to gaze change
Measured head movements varied in size from 1 deg to 97.5 deg (mean±s.e.: 32.9±2.2 deg) but the associated eye-in-head movements rarely exceeded 25 deg (11.9±0.7 deg). The contribution of the eyes to the total gaze was variable and not well predicted by the size of the head movement (Fig. 3A). The eye-in-head movements were unrelated to the head movements ($F_{1,116}$=0.07, P=0.79), sex of the bird ($F_{1,116}$=0.03, P=0.86), or eye that was being monitored ($F_{1,116}$=1.46, P=0.23; Fig. 3A). Horizontal eye movements (mean: 12.1±0.7 deg) were larger than vertical eye movements (6.3±0.5 deg) but they were unrelated to each other ($F_{1,95}$=0.66, P=0.42; Fig. 3B). Eye-in-head movements contributed most to total gaze when total gaze was small ($F_{1,116}$=30.8, P<0.0001); the sex of the birds ($F_{1,116}$=0.23, P=0.63) and the eye being monitored (left or right; $F_{1,116}$=0.16, P=0.69) did not affect the eye contribution (Fig. 3C).

Fig. 4 shows the average time courses for 16 larger head turns (head movements in the range 40–80 deg, mean 53 deg) and 16 smaller head turns (head movement range 0–35 deg, mean 22 deg). In each figure, half of the turns were rostral, in the direction of the beak, and half temporal, away from the beak. Equal numbers were made with open right and left eyes. In the larger turns, the eyes contributed only about 13% of the total gaze change, but in the smaller turns the eye contribution was much larger, approximately 33%. For the larger head movements, the total average duration of the head movement was 0.2 s (12 frames), but the eye-in-head movement was shorter, lasting about 0.1 s, and occupied the first half of the head movement trajectory.
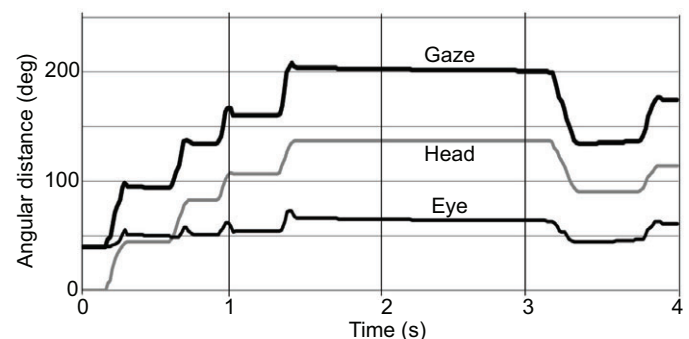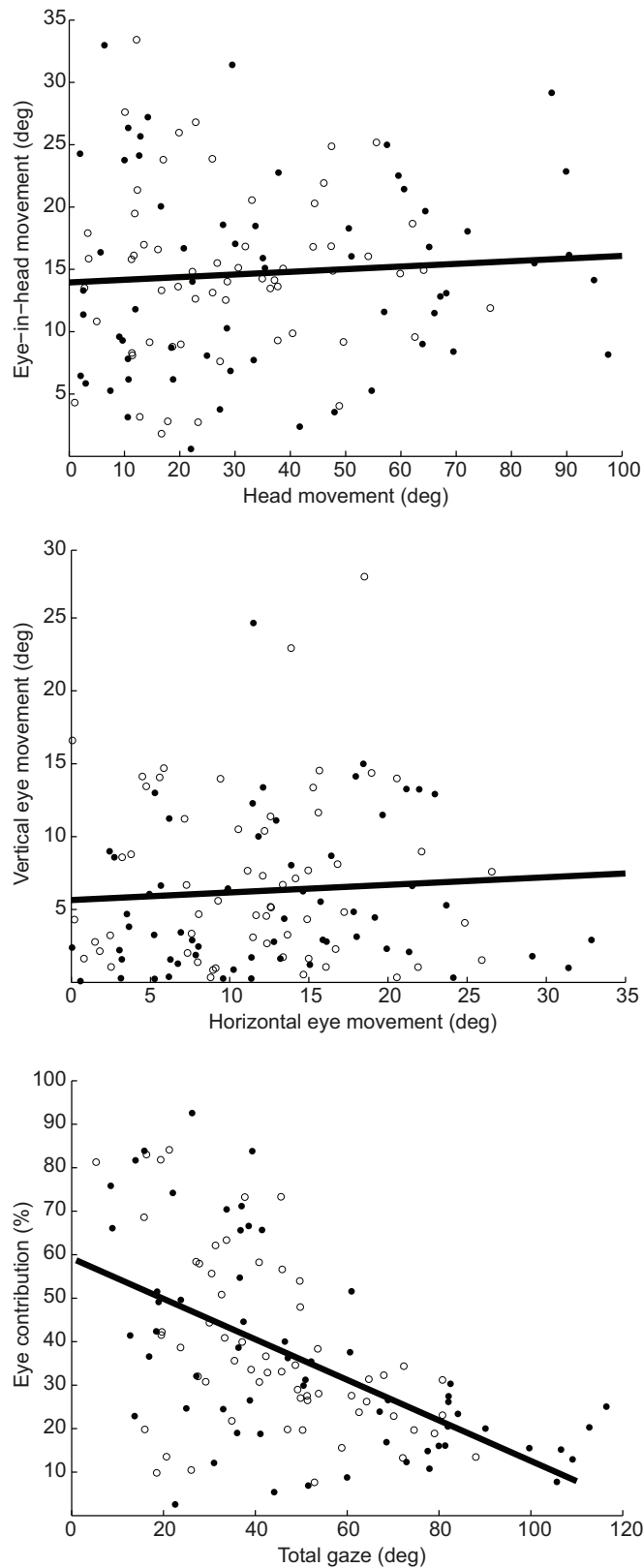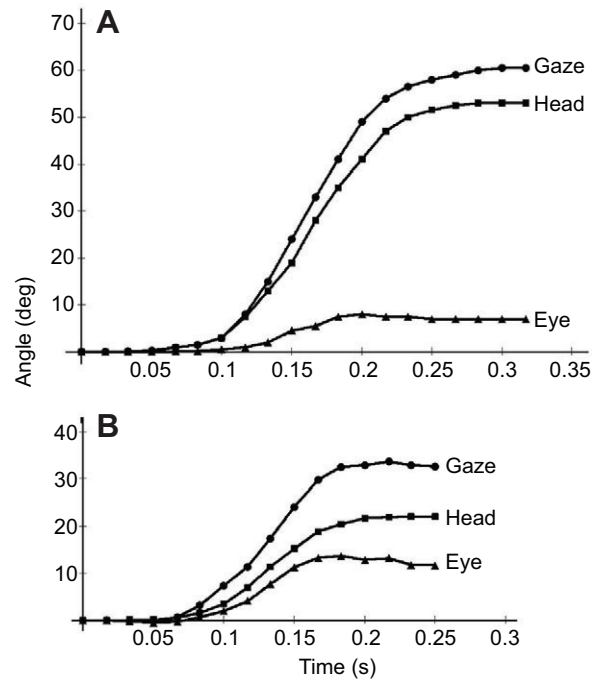

Fig. 2. A sequence of turns. The contributions of eye and head to the gaze changes, and the variability of the fixation intervals between the turns.
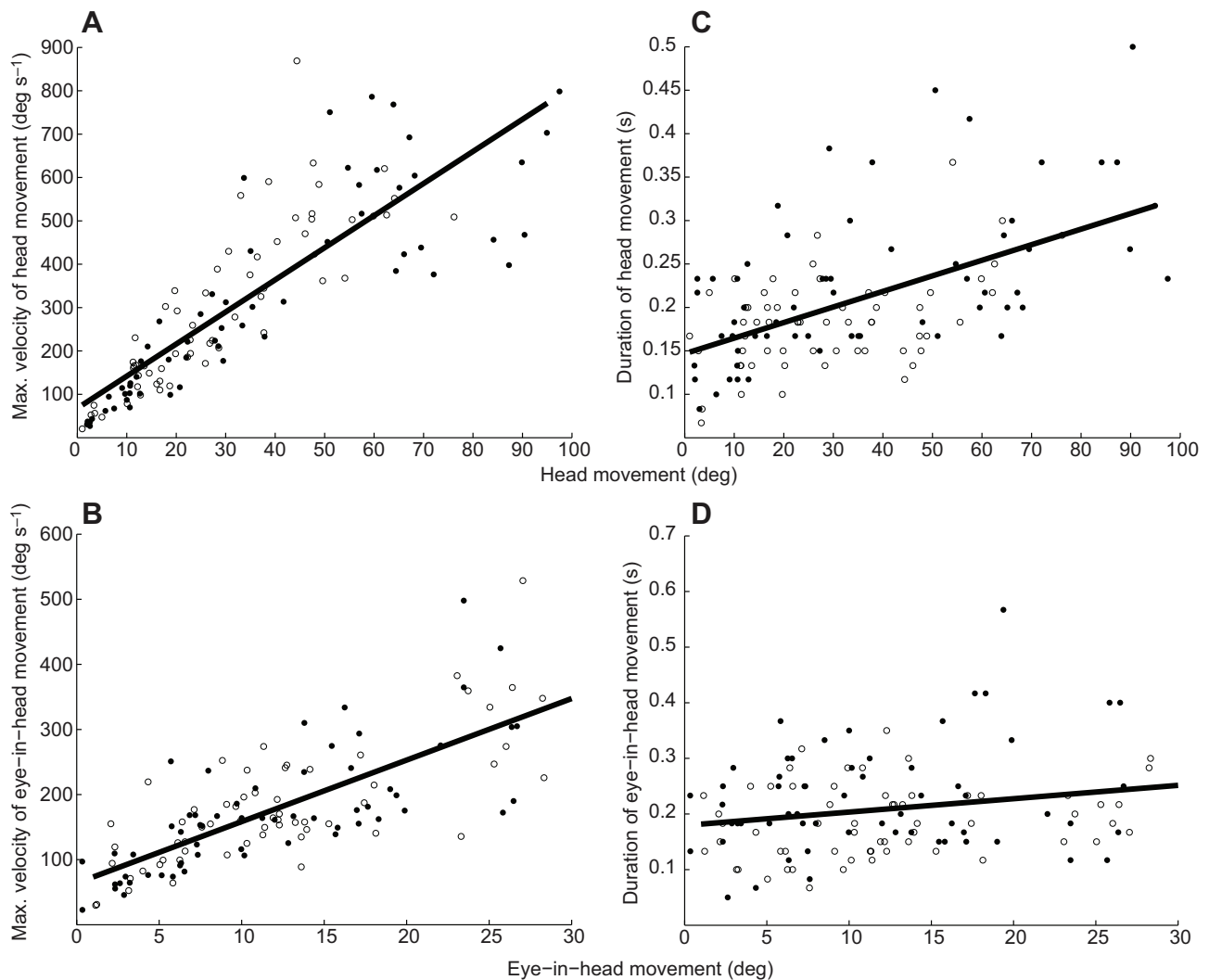
Fig. 4. Large and small gaze shifts. (A) Average time course of 16 larger gaze shifts showing the head, eye-in-head and gaze movements. The contribution of the eye movements to gaze movements is about 13%. (B) Averages for 16 smaller gaze shifts. The head movements are slower and briefer, but the eye-in-head movements are a few degrees larger than those in A (see Fig. 3). Their contribution to the gaze movement is much larger, about 33%.

For the smaller turns, the head movements had shorter durations (0.15 s) and the eye-in-head movements lasted slightly longer than for the larger turns (about 0.12 s, but with much variation). In both the larger and smaller turns there is a hint that the eye counter-rotated by a few degrees in the last part of the turn, but this was not enough to bring the gaze change to a halt, as it does in mammals. This counter-rotation was highly variable, with some eye movement records showing a strong back swing (e.g. Fig. 2, turns 2 and 3 at 0.75 s and 1.0 s), and others nothing at all. If there is a vestibular or optokinetic contribution to the eye movement at the beginning or end of a turn, our data suggest that it is not systematically applied. There did not appear to be quantitative differences between rostrally and temporally directed turns, nor between turns made with the left and right eyes.

The velocities of the head and eye-in-head movements were strongly related to the size of the turn (Fig. 5A,B), with maximum head velocities reaching nearly 1000 deg s^{-1} and maximum eye-in-head velocities reaching nearly 600 deg s^{-1}. The maximum velocities of the head and eye-in-head movements were positively related to the size of the head and eye-in-head movements, respectively (head: $F_{1,116}=296.66$, $P<0.0001$; eye: $F_{1,116}=148.27$, $P<0.0001$) but unrelated to the eye being monitored (head: $F_{1,116}=0.43$, $P=0.51$; eye: $F_{1,116}=0.01$, $P=0.92$). Females had higher maximum velocities of head movements than males (least squares means±s.e.: females 334.3±15.0 deg s^{-1}, males 286.7± 15.6 deg s^{-1}, $F_{1,116}=4.34$, $P=0.04$) but did not differ from males in the velocity of eye-in-head movements ($F_{1,116}=0.13$, $P=0.71$; Fig. 5A,B). However, in the middle size range it is clear from the videos themselves that the turns can be made at different speeds, with a factor of 2 between the fastest and slowest.

Fig. 3. Contribution of head and eye to gaze change. (A) The size of the eye-in-head movements compared with head movements. (B) The amplitude of eye movements in the vertical plane compared with the horizontal plane. (C) The eye contribution relative to total gaze. Open circles are female birds and filled circles are male birds.

Fig. 5. Velocity and duration of head and eye-in-head movements. (A,B) The relationship between the maximum velocity and size of the head movement (A) and eye-in-head movement (B). (C,D) The relationship between the duration and size of the head movement (C) and eye-in-head movement (D). Open circles are female birds and filled circles are male birds.

Head and eye-in-head movement durations also varied with turn size (Fig. 5C,D). The duration of the head movements and eye-in-head movements was positively related to the size of head movements and eye-in-head movements, respectively (head: $F_{1,116}=45.69$, $P<0.0001$; eye-in-head: $F_{1,116}=5.14$, $P=0.025$). Females had shorter durations of head and eye-in-head movements than males (head, least squares means±s.e.: females 0.18±0.01 s, males 0.23±0.01 s, $F_{1,116}=9.68$, $P=0.0023$; eye-in-head, least squares means±s.e.: females 0.18±0.01 s, males 0.24± 0.01 s, $F_{1,116}=12.44$, $P=0.0006$). The duration of the head contribution was unrelated to the eye that was being recorded ($F_{1,116}=2.68$, $P=0.10$) but recordings made from the left eye had shorter durations of eye-in-head movements than those made from the right eye (least squares means±s.e.: left eye 0.19±0.01 s, right eye 0.23±0.01 s, $F_{1,116}=4.28$, $P=0.041$).

Fixation duration
In a sample of 64 intervals between saccades, the majority (73%) had durations of less than 1 s, but there were many longer fixation periods, the longest recorded lasting 6.5 s (Fig. 6). With only one exception (Fig. 7), there were no fixation intervals lasting less than 0.1 s. However, between 0.1 s and 1 s, the intervals were spread

fairly uniformly. Gaze was held stationary during all fixations that we observed.

Variations
Most of the gaze shifts studied conform to the patterns seen in Fig. 4. There were, however, a number of exceptions. One of the most interesting is shown in Fig. 7. One interpretation of this record is that at around 0.12 s the peahen aborts the saccade in order to maintain her current direction of gaze. Despite the ability to cancel the eye movement, it seems she cannot abort a head-turn in progress. She was able to change eye-in-head direction to mirror the head direction, possibly by engaging the VOR (as occurs at the end of large eye-and-head saccades in humans), thereby keeping gaze stationary for about 0.15 s, before eventually allowing gaze to move back at around 0.26 s. The peahen was looking in the direction of the peacock at the time, and it is possible that something in his behavior triggered cancellation of the gaze shift.

DISCUSSION
This is the first study to examine eye and head movements in a freely behaving bird. Both eye and head movements contributed to gaze shifts in Indian peafowl. When gaze shifts were greater, head
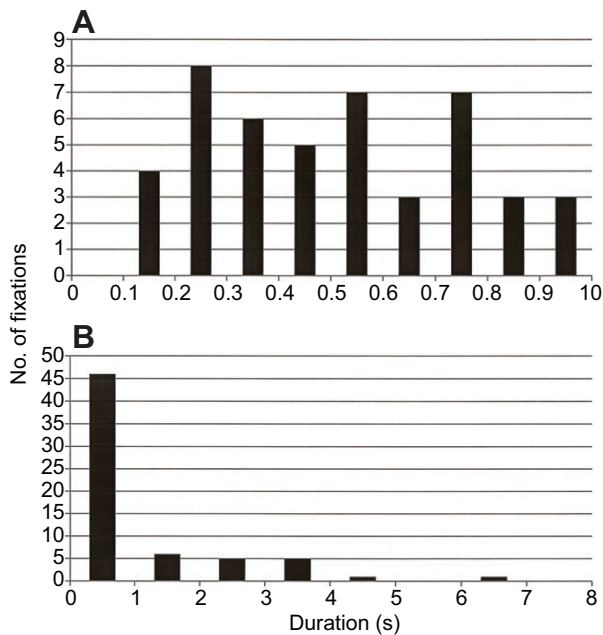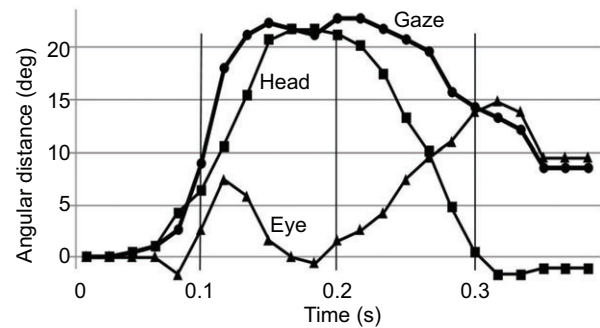
Fig. 6. Duration of fixations. Fixations are defined as intervals between turns. (A) Less than 1 s duration. (B) Longer than 1 s. Sixty-four fixations from two videos, one with the left and one the right eye open.

Fig. 7. Record of a double turn in which the head direction reverses without an interval. The eye (triangles) starts off with the head (as usual) but reverses direction at frame 7 and then for the next 12 frames (0.2 s) moves in the opposite direction to the head (squares). The result is that gaze (circles) stays almost constant – looking in the same direction – for approximately 0.15 s, between frames 7 and 16.

movements were more substantial than eye movements. The duration and velocity of eye and head movements were positively related to saccade amplitude as has been demonstrated in mammals (Bahill et al., 1975). Despite these concordances with mammals, the coordination of eye and head movements in birds differed in some respects from that in mammals.

Eye and head movements influenced gaze changes in peafowl. The amplitude of eye movements in this study (about 10 deg) was similar to that reported for our previous work in freely moving peacocks (Yorzinski and Platt, 2014) and within the range reported for unrestrained pigeons (Wohlschläger et al., 1993). Notably, the amplitude of eye movements in the horizontal plane of peafowl was nearly twice as large as the amplitude of eye movements in the vertical plane. Consistent with these eye movement patterns, we previously found that peahens evaluate potential mates by primarily scanning horizontally (rather than vertically) across the peacock's train (Yorzinski et al., 2013). Because peafowl generally forage on the ground and experience predation by many ground predators (Kannan and James, 1998), scanning horizontally may also facilitate detection of both food items and threats. The amplitude of head movements was generally larger than the amplitude of eye movements in peafowl. It is not surprising that their head movements can be large as they can easily rotate their heads. Similarly, other birds (including peafowl) can drastically shift their field of view by turning their entire body (Land, 2015). It is possible that the birds adjusted their eye and head movements partly in response to wearing the eye-tracker, which blocked portions of their visual field. However, these adjustments (if any) were likely minimal because the cameras each occupied a small area (10 mm×10 mm) and they were positioned in the birds' peripheral fields.

The contribution of eye movements to gaze changes in peafowl was large when gaze changes were small. These results are congruent with eye movement patterns in humans: head movements are infrequent when gaze saccade amplitudes are small (Freedman and Sparks, 2000; Land, 2004). For human gaze changes of up to 30 deg, the head only contributes about 30% (Goossens and van Opstal,

1997), whereas for gaze changes >30 deg, the head contribution increases as the eyes reach their maximum excursion in the orbit. Because head movements are more costly than eye movements, from both a time and energetic perspective (Hardiess et al., 2008), it may be more efficient for birds to shift their gaze with eye movements (rather than head movements) for small gaze changes. Furthermore, large head movements are more conspicuous to predators and conspecifics than eye movements. Peafowl eye movements are not especially conspicuous because the birds have brown irises without a white sclera. To reduce their chances of predation and minimize conspecific aggression, peafowl may favor eye movements over head movements in some contexts, although eye movements were accompanied by at least some head movements.

The coordination of eye and head movements in peafowl differs from that demonstrated in mammals. While peafowl and mammals both shift their eyes and head toward a target (Bizzi et al., 1971; Gresty, 1975; Collewijn, 1977; Guitton and Volle, 1987), in mammals the eyes always reach the endpoint of the gaze shift before the head, and the eyes then invariably counter-rotate so that gaze thereafter remains stationary. This compensation is the result of the VOR induced by the continuing head rotation. Peafowl showed little such compensation, and often none at all. In part, this is because, unlike mammals, the head moves faster than the eye, so that compensation would in any case be less effective. It seems that with some rare exceptions (e.g. Fig. 7), VOR is simply not elicited. Birds do possess a VOR, and a corresponding neck reflex (vestibulo-collic reflex) when the head is involuntarily rotated (Gioanni, 1988b), but we saw little evidence of VOR during natural gaze shifts. In mammals, the maximum eye velocity is similar to that of the peafowl [e.g. 600 deg s^{-1} in rabbits (Collewijn, 1977) compared with 529 deg s^{-1} measured here]. However, many mammals cannot move their heads as quickly as the peafowl [e.g. up to 600 deg s^{-1} in rabbits (Collewijn, 1977) compared with 869 deg s^{-1} measured here], potentially explaining why mammals need a VOR while peafowl do not.

The velocities of the eye and head movements in peafowl were positively related to the eye and head movement amplitudes, respectively. The same pattern is found in humans, such that saccade velocity increases with increasing saccade amplitude ('the main sequence'; Bahill et al., 1975). Because saccade velocities are also related to general arousal (Di Stasi et al., 2013), variation in the peafowl's saccade velocities may have partly been driven by their current physiological and motivational states. The durations of eye and head movements in peafowl were also positively related to eye

and head movement amplitudes, as they are in humans (Bahill et al., 1975). Similar to saccade velocity, saccade duration can also be influenced by other factors. In humans, saccade durations are shorter when subjects shift their gaze toward more meaningful targets (Xu-Wilson et al., 2009).

Peafowl actively shift their gaze toward relevant aspects of their environment, including mates (Yorzinski et al., 2013) and predators (Yorzinski and Platt, 2014). While certain eye and head movements may be constrained by physiological limits and automatic processes, the birds likely exert volitional control over the coordination of some movements. For example, we found that a peahen abruptly changed her eye movements to remain fixating a peacock's display even though her head was already moving in a different direction (Fig. 7). Similar to humans, peahens may also be able to adjust the velocity and duration of their saccades depending on their internal states and motivation. Future studies examining variation in eye and head movements across species will help uncover the factors influencing visually guided behavior.

Author contributions
M.F.L. and J.L.Y. conceived the project and analyzed the data. J.L.Y. collected the data. J.L.Y., M.F.L., G.L.P. and M.L.P. wrote the manuscript.

Supplementary information
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Movie 1. Peahens shift their gaze while freely moving in their environment. The first clip shows a peahen making a small gaze shift. The total gaze shift is 20°, with the head movement contributing 18° and the eye movement contributing only 2°. The second clip shows a peahen making a large gaze shift. The total gaze shift is 60°, with the head movement contributing 33° and the eye movement contributing 27°. The yellow dot indicates where the bird is looking within the environment and the eye movement is displayed in the upper right corner.