RESEARCH ARTICLE

Head-mounted sensors reveal visual attention of free-flying homing pigeons

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ABSTRACT

Gaze behavior offers valuable insights into attention and cognition. However, technological limitations have prevented the examination of animals' gaze behavior in natural, information-rich contexts; for example, during navigation through complex environments. Therefore, we developed a lightweight custom-made logger equipped with an inertial measurement unit (IMU) and GPS to simultaneously track the head movements and flight trajectories of free-flying homing pigeons. Pigeons have a limited range of eye movement, and their eye moves in coordination with their head in a saccadic manner (similar to primate eye saccades). This allows head movement to act as a proxy for visual scanning behavior. Our IMU sensor recorded the 3D movement of the birds' heads in high resolution, allowing us to reliably detect distinct saccade signals. The birds moved their head far more than necessary for maneuvering flight, suggesting that they actively scanned the environment. This movement was predominantly horizontal (yaw) and sideways (roll), allowing them to scan the environment with their lateral visual field. They decreased their head movement when they flew solo over prominent landmarks (major roads and a railway line) and also when they flew in pairs (especially when flying side by side, with the partner maintained in their lateral visual field). Thus, a decrease in head movement indicates a change in birds' focus of attention. We conclude that pigeons use their head gaze in a task-related manner and that tracking flying birds' head movement is a promising method for examining their visual attention during natural tasks.

KEY WORDS: Flocking, Head movement, *Columba livia*, Inertial measurement unit, Navigation

INTRODUCTION

Like humans and many other animals, birds rely on vision to guide their behavior. Previous studies have examined how birds use visual information during various natural activities such as tracking and catching prey (Brighton et al., 2017; Land, 1999b), detecting predators (Fernández-Juricic, 2012; Jones et al., 2007) and recognizing landmarks during navigation (Biro et al., 2004; Lipp et al., 2004; Martinho et al., 2015; Pritchard et al., 2018). However, we are still lacking a detailed understanding of how birds strategically deploy vision to gather relevant information about the natural environment: existing studies are largely limited to inferring visual attention during navigation from flight trajectories (e.g. Guilford et al., 2004), electroencephalography (EEG)

recordings (Vyssotski et al., 2009) and head tilts (Rattenborg et al., 2016), to direct observations of head movement in the field during vigilance and prey pursuit (e.g. Fernández-Juricic, 2012; Land, 1999b), or to detailed analyses of head movement in the laboratory to analyze its basic functions, such as gaze stabilization (e.g. Aldoumani et al., 2016; Troje and Frost, 2000; Warrick et al., 2002). A few exceptions are Kane and Zamani (2014), Kane et al. (2015) and Brighton et al. (2017), who used head-mounted cameras to examine the gaze behavior of frontally eyed birds of prey, such as hawks and peregrines, albeit limited to the context of prey pursuit over short distances. Currently lacking is the study of gaze behavior during long-range navigation and in laterally eyed birds such as pigeons. In the present study, we developed state-of-the-art miniature head-mounted sensors for pigeons to examine how these birds use their gaze while orienting through visually complex natural environments.

A common method for examining visual attention in human and nonhuman mammals is eye-tracking, which can record the orientation of a subject's gaze with high temporal and spatial resolution. This technology can offer valuable insights into attention and cognition in non-verbal or pre-verbal subjects such as human infants (Gredebäck et al., 2009), great apes (Kano et al., 2017), monkeys (Ghazanfar and Shepherd, 2011) and dogs (Téglás et al., 2012). Like primates, birds also have only limited parts of their retina specialized for higher visual acuity (i.e. the fovea), and they foveate a visual target by shifting their head and eye (i.e. gaze) (Dawkins and Woodington, 2000; Fernández-Juricic, 2012). For birds, a method equivalent to eye-tracking can be provided by head-tracking. This is because while most primate species have a high degree of eye movement, most bird species have a limited range of eye movement and instead rely on head movement to shift their gaze. Laboratory studies have shown that although the range of eye positions can exceed 20 deg (in non-head-restrained pigeons), it is typically approximately 2–3 deg during walking (Wohlschläger et al., 1993; Haque and Dickman, 2005). A recent experiment incorporating both head and eye tracking in pigeons confirmed that during flight the range of eye positions is predominantly confined to 5 deg (I. Ross, personal communication). During feeding, such as pecking at grain, pigeons use their eyes to maintain visual fixation (in their frontal vision) by converging both eyes onto individual targets at an angle according to the distance between their eyes and the target. Critically, pigeons show almost perfect temporal coordination between head and eye movement during both walking and feeding: head movement accounts for over 90% of overall gaze shifts, and eye movement only supports head movement (Gioanni, 1988; Haque and Dickman, 2005; Wohlschläger et al., 1993). Although the degree of eye movement varies significantly between species, such head–eye coordination is commonly observed in other birds such as chickens (Pratt, 1982) and quails (Haque and Dickman, 2005). Additionally, most bird species move their heads in a saccadic manner, with periods of fixation between saccades,

similar to primate eye movement (Land, 1999a). Between saccades, the head orientation of birds is stabilized in all rotational axes (yaw, roll and pitch) without eye movement, both during flying (Eckmeier et al., 2008; Green et al., 1992; Kress et al., 2015; Ros and Biewener, 2017) and walking (Eckmeier et al., 2008; Gioanni, 1988; Haque and Dickman, 2005; Kress et al., 2015; Wohlschläger et al., 1993). The role of such stabilization is likely the minimization of motion blur in retinal images between saccades (Land, 1999a). Because of these features, head movement is often used as a proxy for gaze movement in studies of bird vision, although the projected direction of gaze (or fovea) can differ between laterally eyed birds (Eckmeier et al., 2008; Green et al., 1992; Kress et al., 2015; Ros and Biewener, 2017) and frontally eyed birds (Brighton et al., 2017; Kane et al., 2015; Kane and Zamani, 2014).

Although the visual system of birds has much in common with that of primates, there are some important differences that need to be taken into consideration when we interpret avian gaze behavior. Many species of birds, particularly laterally eyed birds of prey, have two foveae in each eye, one specialized for viewing objects frontally and the other for viewing objects laterally (Maldonado et al., 1988). Previous studies have examined the patterns of head movement in pigeons and chickens while they were pecking, stationary, walking, landing and flying over a short distance. They found that these laterally eyed birds tend to use their frontal visual field when examining a stationary or slow-moving object at close range (e.g. during pecking and landing) and use their lateral visual field when examining a fast-moving object or an object at a greater distance (Dawkins, 2002; Erichsen et al., 1989; Maldonado et al., 1988). Unlike mammals, birds such as pigeons, chickens and finches view the movements of objects mostly with a stationary head and eye, although some predatory bird species track their prey with smooth head movements (Land, 1999b). Furthermore, one study showed that when chickens spotted a novel object on the ground, rather than staring straight at it (as a primate would), they continued to move their head and eyes to such a degree that they appeared to be examining it with a different part of the retina (Dawkins, 2002). Given these differences, to accurately evaluate the visual attention of birds, it is crucial to understand what aspects of their head movements are most relevant to their visual attention.

This study had two complementary goals. Our first goal was to establish a new method of tracking visually guided behavior in pigeons in the field through simultaneous recordings of head movements using an inertial measurement unit (IMU) and flight trajectories using global positioning system (GPS) during homing flights. Although lightweight GPS devices have become well established as a reliable technology for tracking moment-to-moment changes in the flight trajectories of pigeons (Biro et al., 2004; Dennis et al., 2007; Gagliardo et al., 2011; Guilford et al., 2004; Lipp et al., 2004; Martinho et al., 2015; Portugal et al., 2017; Schiffner and Wiltschko, 2009), the use of an IMU to track head movement has never been attempted in the field. IMUs are equipped with an accelerometer, a gyroscope and a magnetometer, and hence can provide highly accurate reconstructions of motion and turns; they can also provide an estimate of absolute orientation with respect to gravity and the Earth's magnetic field (e.g. north). Aldoumani et al. (2016) used an IMU system to track the 3D head movement (yaw, roll and pitch) of pigeons in the laboratory and found that the system was able to more reliably track subjects' head movement than video-tracking analysis.

Our second goal was to conduct a systematic series of releases with homing pigeons to reveal patterns in, and functions of, head movements during large-scale navigation through natural environments. Specifically, we examined how birds adjust their gaze behavior in relation to their own flight maneuvers and the visual cues in the environment. More specifically, we examined how they changed the pattern of their head movement (i) when they were in straight, steady flight compared with when they were on the ground, or when they made steep turns during flight, (ii) over the course of learning a specific route through repeated flights over the same terrain, (iii) when they flew over prominent visual landmarks such as major roads, identified as key visual cues in previous studies (Biro et al., 2004; Lipp et al., 2004) and (iv) when they flew with a partner, i.e. when a prominent visual target was introduced, and/or vigilance and navigational tasks could be shared with a conspecific.

MATERIALS AND METHODS
Subjects
Twenty-two homing pigeons (*Columba livia*; Gmelin, 1789) bred at the Oxford University Field Station at Wytham, UK (51°46′58.34″N, 1°19′02.40″W), were used in this study. All pigeons were between 1 and 11 years old (4.1±2.5 years; mean±s.d.) and weighed 443±25 g (mean±s.d.). They lived in two adjacent lofts home to a social group of ∼140 pigeons, and received *ad libitum* food, water and grit daily throughout the study. All were experienced with homing to the loft from sites up to 10 km, but had not been released from the vicinity of the current release site. The study protocols were approved by the Local Ethical Review Committee of the University of Oxford's Department of Zoology (no. APA/1/5/ZOO/NASPA/Biro/PigeonsHeadmountedsensors).

Apparatus
To record pigeons' head movements and flight trajectories simultaneously, we built a custom-made 'pSensor' logger. The device weighed 21.7 g, 1 g of which was the head unit (Fig. 1A), and was equipped with a microcomputer (Feather, Adafruit, New York, NY, USA), GPS (Adafruit Ultimate GPS, −165 dBm sensitivity, 66 channels; positional accuracy <3 m, velocity accuracy <0.1 m s^{-1}), nine-axis IMU sensor (a combination of gyroscope, accelerometer and magnetometer; BNO055 Absolute Orientation Sensor, Adafruit), a micro-SD card (32 GB; SanDisk, Milpitas, CA, USA) and a battery (110 mAh, 3.7 V, giving a battery life of approximately 1.5 h). This logger was able to record GPS data at 10 Hz and IMU data at 60 Hz. The sampling frequency of our GPS, 10 Hz, is the highest among currently available GPS devices, and has been shown to be able to reconstruct pigeon flight trajectories with high accuracy during both solo and group flights (Flack et al., 2013; Nagy et al., 2010; Pettit et al., 2013). We did not record altitude in order to improve the logging rate (using the minimum GPS sentences) and because of the known inaccuracies of GPS altitude data. The sampling frequency of our IMU device, 60 Hz, is commonly used in eye-tracking of primates and is able to reconstruct saccadic movements (Duchowski, 2007; Krupenye et al., 2016); note that speed of a bird head saccade is similar to, or slightly slower than, that of a primate eye saccade (Fuchs, 1967; Wohlschläger et al., 1993). The IMU sensor was glued to a custom-built mask (3.8 g) made to fit each subject's unique head shape. This mask was made of wires, felt and elastic bands. The mask was fitted to the bird's head sufficiently firmly that it could not slip out of place or be shifted by the wind or the bird's head movement. The mask had two fixation points: the root of the beak (by an arch-shaped solid wire) and the back of the head (by an elastic band extended from the connections to the bottom of the arch-shaped wire). Importantly, no part of the mask was near the bird's throat so as to avoid any interference with breathing (Fig. 1B,C). The IMU

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Fig. 1. The 'pSensor' logger. (A) GPS logger, microcomputer, micro-SD card and battery (left; to be carried in a backpack) connected to an inertial measurement unit (IMU) mounted on the custom-made mask (right; to be carried on the head). (B,C) A pigeon wearing the mask and logger.

sensor was glued to the flattest upper surface of the mask, and the roll axis of the sensor was roughly parallel to the line connecting the root of the upper beak and the back of the head (the center of the occipital crest). The shape of the mask was customized for each bird so that the mask was positioned identically every time it was worn by the bird. The IMU sensor was connected via four thin cables (26–28 AWG) to the remainder of the unit, which was carried in a backpack made of lightweight fabric and elastic straps (3 g). Including the mask, backpack and pSensor, pigeons carried a total of 28.5 g. Calibration was conducted before each release by following a standard procedure for this IMU device (the device was kept still for a few seconds in a minimum of six orientations).

Procedure
Habituation to wearing the mask and backpack
All birds were habituated to wearing the custom-made mask and backpack prior to flight testing. Backpacks were individually fitted to birds following established procedures (Nagy et al., 2010), to be worn for the duration of the study, and we verified that birds were able to walk and fly normally whilst wearing them. Many of the current subjects were already familiar with these backpacks from recent experiments (e.g. Sasaki and Biro, 2017; Taylor et al., 2017; Watts et al., 2016). Birds typically preened the elastic straps to their breast feathers; we checked these daily to ensure they had not slipped. Mask habituation lasted a minimum of 7 days (with each daily session lasting a maximum of 4 h) inside or around the birds' home loft. For safety and comfort, masks were designed such that birds could take them off by themselves using their feet, so the purpose of the habituation sessions was to accustom them to masks to the point that they stopped removing them. The criterion for a bird passing habituation was that it did not take the mask off on two consecutive days out of a total of 7 days. No bird was dropped from the study for failing to meet this criterion. After 7 days of habituation, birds rarely removed the mask, although they occasionally made apparent attempts to do so (e.g. by shaking their head), particularly at the beginning of a daily session. However, we confirmed that the frequency of such attempts decreased considerably within the first hour of the session (typically 4 times per hour in the first hour to 0–1 times per hour in the remaining hours). Importantly, after the 7 days of mask habituation, we confirmed that all birds exhibited normal locomotive patterns (e.g. walking, flying, landing, taking off) and other essential activities (e.g. drinking, eating, tending to chicks/eggs) inside and around the loft.

Testing
All flights in this study were from a site 3.82 km north of the home loft (51°49′02.85″N, 1°18′50.05″W; bearing to the loft, 185.1 deg).

Each pigeon performed one homing flight per day, on days when the sun's disc was visible, and wind speeds were below 7 m s^{-1}. On the days of testing, each bird was fitted with the mask at the home loft. After 30 min of habituation to the mask inside the loft, they were transported to the release site by car. At the release site, the IMU sensor was calibrated and then attached to the mask of each bird. The birds were released facing the home direction, a minimum of 5 min after confirming that the previously released birds had disappeared from view. The masks were removed soon after birds arrived at the loft.

The releases were conducted in three phases. We first released each bird singly eight times (phase 1 solo flights), to analyze head movements during individual navigation and route learning. The number of flights in this phase was chosen based on previous work which showed that the greatest route learning effects (evidenced by the emergence of shorter, more efficient routes) are observed in the first four to six flights from a novel release site, and that by the eighth flight birds have settled on preferred routes that they recapitulate without much evidence of further improvement (Meade et al., 2005; Pettit et al., 2013; Taylor et al., 2017). Furthermore, previous studies from similar terrains have reported that pigeons have a strong tendency to use linear structures, such as roads and railway lines (Biro et al., 2004; Lipp et al., 2004; Vyssotski et al., 2009). The solo releases thus also allowed us to examine how our birds changed the pattern of their head movement near such structures; our birds flew across two major roads (A44 and A40) and a railway line on the way to the loft.

We then released subjects in pairs (phase 2, paired flights) to examine whether patterns in birds' head movements change when a prominent visual target (the flight partner) is introduced, and when vigilance and navigational tasks can be shared with a conspecific. Each bird flew nine paired releases, and pairs were constructed in a trial-unique manner, i.e. no bird flew with the same partner more than once. Finally, we conducted two more solo trials (phase 3 solo flights) to ensure that any key differences observed between phases 1 and 2 were not caused by continued route learning (but by the presence of the partner). The logger failed to record data in a total of 10 trials (four phase 1 solo and six phase 2 paired flights), owing to a break in its circuit, and thus these flights were treated as missing data (including the partner's data in paired flights). In addition, those paired flights in which the birds did not flock (defined as the two birds spending more than 50% of the total flight time at distances greater than 200 m from each other) were excluded from the analysis. The value of 200 m was based on previous experiments that confirmed this distance as the limit for two birds to interact during flight (Biro et al., 2006; Pettit et al., 2013). In all, we obtained data for a total of 172, 172 and 44 flights for phases 1, 2 and 3, respectively.

Data analysis

The head-mounted sensor records the head movement of the birds with respect to the environment (i.e. in an inertial reference frame, not with respect to the body). Three-dimensional movements of the head can be analyzed as the rotational movements along three axes: yaw, roll and pitch (Fig. 2). The gyro sensor estimates the angular velocity (deg s^{-1}) in yaw, roll and pitch. The integration of those angular velocities yields the angles of each axis (Fig. 2C). The combined angular velocity was calculated as $\sqrt{y^2 + r^2 + p^2}$, where y, r and p are yaw, roll and pitch angular velocity, respectively (Fig. 2D). Spikes in the combined angular velocity indicate head saccades. A saccade was defined if the combined angular velocity exceeded 60 deg s^{-1} and the saccade duration was longer than 50 ms (see Fig. S1). Some birds occasionally shook their head during flights; these events were detected as large head saccades (defined as combined angular velocity >800 deg s^{-1}) and were removed from the analysis. We defined saccade amplitude as the angular distance traveled by the head in each saccade, saccade frequency as the mean number of saccades per second, and head angular velocity as the combined angular velocity calculated by including only saccadic periods. Note that the head angular velocity is the combined value of the saccade frequency and amplitude (i.e. saccade amplitude×frequency). In the human eye-movement literature (e.g. Henderson, 2003), both frequency and amplitude of saccades are often reported because those two measures convey slightly different meanings; the former indicates how long an individual attended to one location over another (i.e. timing), whereas the latter indicates how large the area is that the subject scanned (i.e. size).

We also analyzed the absolute orientations (i.e. Euler angles relative to gravity and magnetic north) using fused sensor data
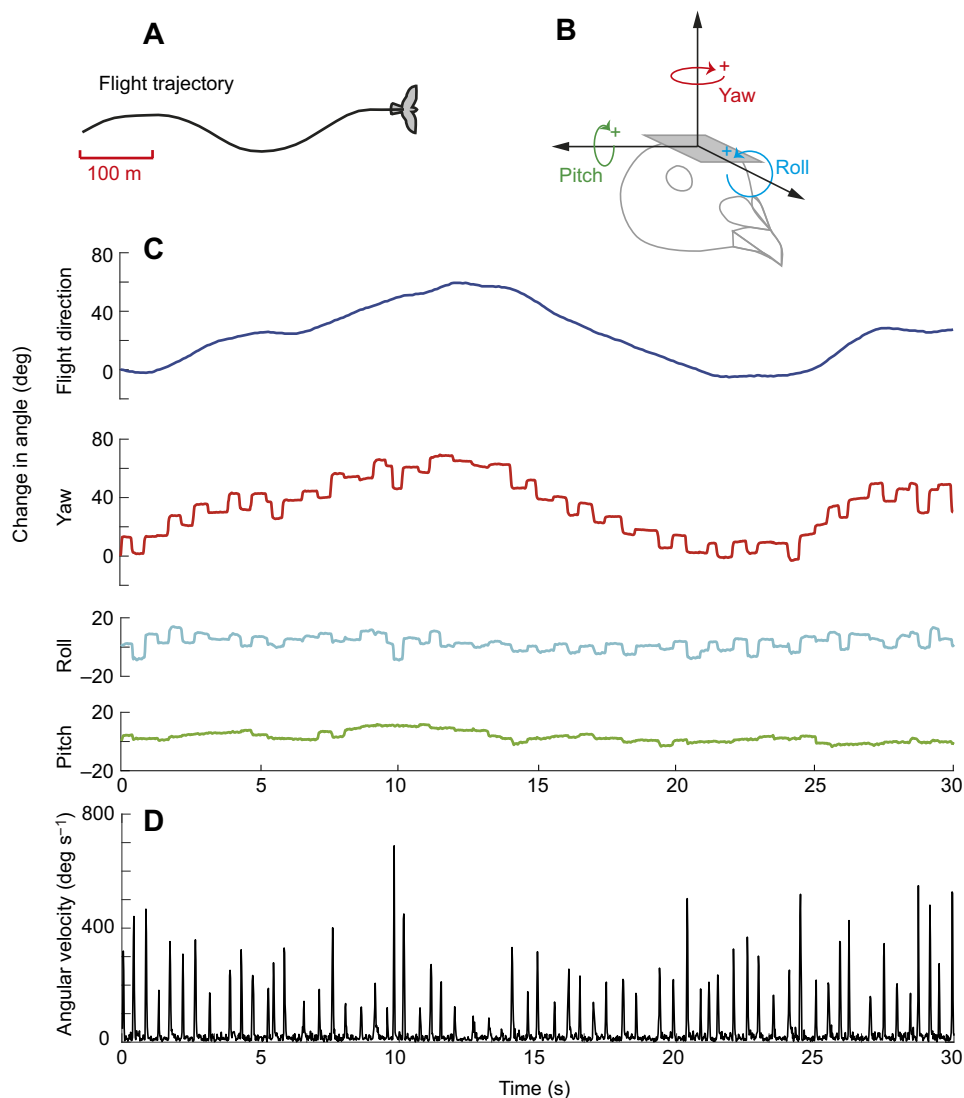

Fig. 2. An example 30-s flight segment (~500 m) recorded by the pSensor. (A) Flight trajectory recorded by the GPS. (B) Three-dimensional movements of the head recorded by the IMU, represented as yaw, roll and pitch. The arrows indicate the direction of rotation. (C) Changes in flight direction (deg; recorded by the GPS), and yaw, roll and pitch angle of the head (deg; recorded by the IMU). (D) Changes in velocity (deg s^{-1}) of the head in the combined angle, defined as $\sqrt{y^2 + r^2 + p^2}$, where y, r and p are gyro-speed of yaw, roll and pitch, respectively. For a video showing simultaneous head movement and trajectory reconstruction, see Movie 1.

provided by our IMU sensor (Fig. 3). Integrated gyro data is insufficient to provide absolute orientation due to the accumulation of small drifts in recordings lasting several minutes. Our IMU sensor provided real-time calibration accuracies of the system on a scale from 0 (failed) to 3 (very good). Unfortunately, this calibration does not work when quick movements of the head are performed (e.g. head shaking). However, the system calibration was 3 for 49% of the full solo tracks and 11% of the full paired tracks. These data
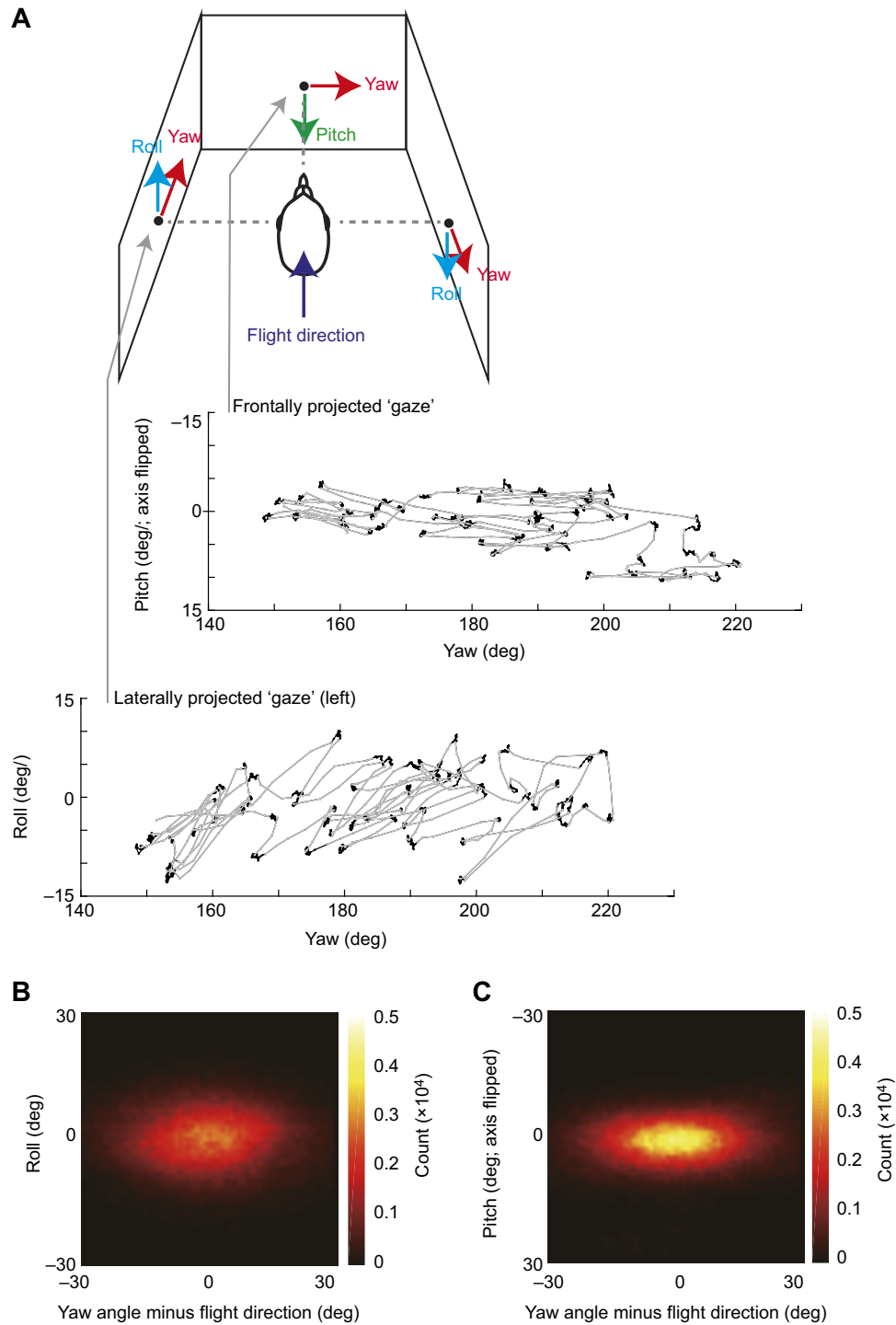
Fig. 3. Movement of the center points of the frontal visual field (yaw against pitch) and the lateral visual field (yaw against roll). (A) Examples of such movement. Gray and black circles represent the samples classified as saccades and inter-saccade intervals, respectively. (B,C) The distribution of the center points of the frontal (B) and lateral (C) visual field. These data are from all 22 birds during the solo flights.

still allow us to describe the overall patterns of absolute orientation by pooling all the collected data. We used the normalized values for the analysis so that the means of the roll or pitch orientation, and the difference between the yaw orientation and flight direction were adjusted to zero in each flight.

The GPS data were processed by cropping the track to include only samples in which instantaneous ground speed was greater than 10 km h^{-1} (i.e. flight). We then excluded samples during taking off and landing from the flights by removing periods in which the bird was within 50 m of the release site or the loft. The data were then filtered by detecting the spikes in the derivatives of each coordinate (longitude and latitude), and we smoothed each coordinate using a 1-s moving window. The data were then interpolated to 60 Hz and synchronized with the head-movement IMU data (60 Hz). Finally, we converted longitude and latitude to meters (X and Y) using a Universal Transverse Mercator projection. Instantaneous flight direction was defined as the vector pointing from the previous to the current coordinate. Note that this instantaneous flight direction is the bird's ground vector and will be offset from its air vector (the body orientation) owing to wind. Ground speed and rate of change in flight direction were defined as the momentary changes in coordinate (km h^{-1}) and flight direction (deg s^{-1}), respectively. Distances from major roads (A44 and A40) or the railway line were calculated for each sample as the straight-line distance from the given bird to the road/railway; those linear features were determined as a series of line segments plotted using an online map and custom program. In the paired flights (phase 2), we excluded the periods in which the focal bird was separated from the partner bird farther than 200 m (unless these represented more than 50% of the total flight time, in which case the entire flight was removed from the analysis, as described above).

Previous studies confirmed that a GPS device can reliably capture pigeons' turns and speeds (or relative changes in direction and position) in both solo and group flights (for these validations, see previous studies by Flack et al., 2013; Nagy et al., 2010; Pettit et al., 2013; and also see Brighton et al., 2017 for validation in the context of studying peregrine falcons' prey pursuit). However, in general, GPS cannot reliably capture small-scale movements in pigeons' flight paths (on a scale of <3 m) because of the inherent inaccuracies associated with this technology and the built-in filtering method. An additional IMU mounted on the bird's body may compensate for such inaccuracies if the IMU data are combined with the GPS data, but it was not used in this study owing to weight restrictions. Previous studies using back-mounted accelerometers revealed that, during flapping (3–10 Hz), pigeons show substantial vertical accelerations (Taylor et al., 2017; Usherwood et al., 2011), which may induce small correction movements of the head and may actually explain the short and small saccades (<50 ms, <4 deg) that we frequently observed in this study (Fig. S1). Because such small saccades were not reliably distinguishable from noise and were likely unrelated to visual scanning (but likely related to correction for gaze stabilization), we filtered them out in the data analysis.

To compare the pattern of head movement when the birds were in flight versus when they were standing still on the ground, we sampled periods in which the ground speed dropped below 10 km h^{-1} in the vicinity of the loft (indicating that the bird was landing or had landed). To make sure that the bird was indeed on the ground, we removed the first minute of the cropped data. We then selected the next 3 min of the cropped data and from this removed the periods in which the bird was either walking or had taken off again (4% of the 3-min datastreams) by detecting the translational movements in the accelerometer. Head-bobbing while walking was

thus not included in our analysis (for the description of this behavior, see Davies and Green, 1988; Green et al., 1992; Troje and Frost, 2000).

Statistical analyses were conducted in R (version 3.2.0; https://www.r-project.org/). To test the difference in behavior between a pair of conditions (e.g. solo versus paired flights), we used paired *t*-tests. To test linear trends in behavior across multiple variables (e.g. over the repeated flights), we used linear mixed models (LMMs) with Gaussian error structure and identity link function using the R package 'lme4'. We included subject as a random factor affecting the slopes and intercepts of fixed factors. We tested significance using a likelihood-ratio test comparing the full model with a model without the effect in question. We checked the assumptions of Gaussian error and homogeneous variance by visual inspection of plotted residuals in these tests.

RESULTS

The head-mounted IMU of pSensor was able to reliably detect the pigeons' head movement during flight. Calculating the combined angular velocity of yaw, roll and pitch rotations revealed clearly distinctive 'spikes' in the data, which indicate saccadic movement of the head (Fig. 2D). To describe the basic patterns of saccades, we pooled all the saccades detected from all our subjects during solo flights ($n=11.0\times10^4$). During saccades, the mean angular velocity of the head was 150.6±65.0 deg s^{-1} in the combined angle (±s.d.; 96.6±62.3 deg s^{-1} in yaw, 93.2±61.9 deg s^{-1} in roll, 26.2±22.0 deg s^{-1} in pitch), whereas it was much slower during inter-saccadic intervals, 21.3±19.4 deg s^{-1}, in the combined angle (8.8±12.7 deg s^{-1} in yaw, 11.0±14.3 deg s^{-1} in roll, 12.0±11.0 deg s^{-1} in pitch). The duration of each saccade was 0.07±0.03 s (±s.d.). The inter-saccadic interval varied greatly in duration, and the amplitude of each saccade also varied greatly in size (Fig. S1). Importantly, these values varied systematically according to the birds' flight maneuvers as well as the visual cues in the environment, as detailed below. Our IMU sensor could also record absolute head orientations (Fig. 3A), although only half of the recordings gave accurate readings (i.e. where system calibration was 3) during solo flights. To describe the basic patterns of absolute head orientations, we pooled all the samples with system calibrations of 3 during solo flights ($n=17.6\times10^5$). The birds oriented their head to a maximum of approximately ±30 deg in yaw (relative to the flight direction; ±21.1 deg s.d.; Fig. 3B), ±20 deg in roll (relative to gravity; ±17.3 deg s.d.) and ±10 deg in pitch (±7.6 deg s.d.; Fig. 3C). These results indicate two main points. First, the birds moved their heads far more than necessary for the changes in flight direction (i.e. the yaw orientation was distributed widely around the flight direction). Second, the birds moved their heads predominantly in the yaw and roll axes (i.e. horizontal and sideways-tilting movement) and less so in the pitch axis (i.e. up–down movement; Fig. 2C; Table 1). Greater roll than pitch movement of the head allows birds to shift the lateral visual fields more than the frontal visual field (compare Fig. 3B and C).

We then compared these characteristics of head movement with two additional contexts: when the birds were (i) stationary on the ground and (ii) making steep turns during flight. While standing still, birds moved their head overall more compared with when they were flying, especially in the yaw direction (Table 1), likely indicating that the yaw movement was, to some degree, constrained during flight. When the birds turned more steeply during flight (i.e. as the rate of change in flight direction increased), they increased their head movement in the yaw direction but decreased it in the roll direction (Fig. S2). The analysis of contingency between the yaw

Table 1. Summary of head-movement results when birds were stationary on the ground, flying alone, flying in a pair and flying alone after completing all the paired flights

	Ground	Solo	Pair	Solo after pair
Saccade frequency (saccades s^{-1})	1.21±0.03	1.74±0.04	1.47±0.04	1.79±0.03
Saccade amplitude (deg saccade^{-1})	24.24±0.41	12.65±0.32	9.51±0.25	12.44±0.38
Yaw	19.57±0.44	8.13±0.22	5.63±0.14	7.83±0.21
Roll	8.35±0.29	7.84±0.31	6.05±0.23	7.84±0.41
Pitch	6.00±0.36	2.15±0.07	1.96±0.06	2.18±0.07
Head angular velocity (frequency×amplitude; deg s^{-1})	29.21±1.02	21.96±0.76	14.12±0.62	22.32±0.90
Rate of change in flight direction (deg s^{-1})	–	7.67±0.26	6.87±0.11	6.99±0.31
Flight speed (km h^{-1})	–	52.65±1.20	49.00±0.59	61.60±0.80
Homing efficiency (proportion)	–	0.72±0.02	0.85±0.01	0.81±0.02

Values are subject means (±s.e.m.) from all birds.

head orientation and flight direction (Fig. S3) revealed that (i) when birds turned either left or right, they oriented their head (in yaw) slightly toward the corresponding direction (mean±s.d. was 5.5± 21.7 and 5.4±20.0 deg for left and right turns, respectively), but (ii) when they turned more steeply (up to 30–40 deg s^{-1}), they oriented their heads (in yaw) to a more pronounced degree toward the corresponding direction (Fig. S3), consistent with previous findings from a laboratory setting (Ros and Biewener, 2017). As a result, changes in head angle consistently preceded changes in flight direction by about half a second, irrespective of the rate of change in flight direction.

We next examined how birds in flight changed the pattern of their head movement according to experience and the presence of specific visual cues in the environment. First, we examined the pattern of changes over consecutive releases. Birds sharply increased their homing efficiency (the beeline distance between the release site and the loft divided by the length of the path flown) over consecutive flights (LMM, χ^2=24.4, d.f.=1, P<0.001; Fig. 4A). Moreover, nearest-neighbor distances between successive flights decreased progressively (χ^2=17.9, d.f.=1, P<0.001), indicating the establishment and recapitulation of individually preferred routes (Fig. 4B). These changes occurred mostly over the first four flights. Changes in head movement over successive releases were small
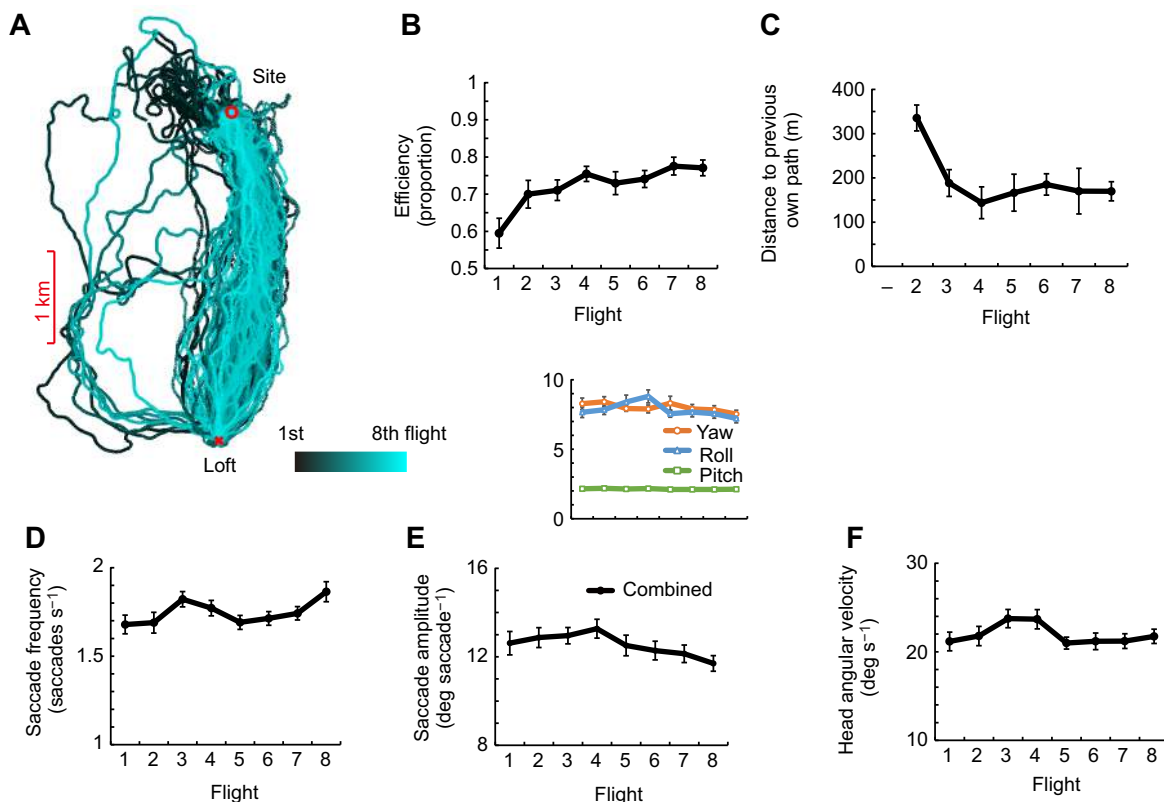
Fig. 4. Flight performance and head movement as a function of solo release number. (A) Flight trajectories of all 22 birds during solo flights. Lighter color indicates a later flight from the same release site. (B) Homing efficiency (defined as the beeline distance between the release site and the loft divided by the length of the path flown). (C) Average nearest-neighbor distance to previous path. Decrease in the distance to a bird's own previous track indicates the appearance of route recapitulation. (D–F) Head movement characteristics: saccade frequency (D), saccade amplitude (E and inset) and head angular velocity (frequency×amplitude; F). Values are subject means (±s.e.m.) from all 22 birds during solo flights.

overall: birds did not change the rate of head turning over consecutive flights ($\chi^2=0.70$, d.f.=1, $P=0.40$; Fig. 4C). Yet, when we restricted our analysis to the first four flights, during which the route learning occurs most prominently, we found that the rate of head turning increased ($\chi^2=16.2$, d.f.=1, $P<0.001$; Fig. 4D), with higher saccade frequency ($\chi^2=9.8$, d.f.=1, $P=0.002$; Fig. 4E) and saccade amplitude ($\chi^2=4.7$, d.f.=1, $P=0.03$; Fig. 4F). After the first four flights, the birds did not increase their homing efficiency ($\chi^2=3.6$, d.f.=1, $P=0.059$) or decrease the distance from their previous paths ($\chi^2=0.0$, d.f.=1, $P=0.96$), and did not change the rate of head turning over consecutive flights ($\chi^2=2.3$, d.f.=1, $P=0.13$).

Second, we examined how the birds changed the pattern of their head movement when they flew across prominent visual features in the landscape, such as two major roads and a railway line that passed across the terrain between the release site and the home loft. Consistent with previous studies (Guilford et al., 2004; Schiffner and Wiltschko, 2009), we saw an increase in the rate of change in flight direction (or tortuosity; LMM, $\chi^2=35.6$, d.f.=1, $P<0.001$; Fig. 5B) and a decrease in ground speed ($\chi^2=32.1$, d.f.=1, $P<0.001$; Fig. 5C) on approach and leave of these linear landmarks during solo flights. In addition, we found that the birds decreased their rate of head turning ($\chi^2=15.6$, d.f.=1, $P<0.001$; Fig. 5D), with lower saccade frequency ($\chi^2=11.7$, d.f.=1, $P<0.001$; Fig. 5E) and saccade amplitude ($\chi^2=9.9$, d.f.=1, $P=0.002$; Fig. 5F) the closer they were to the roads/railway line during solo flights.

Third, we examined how the birds changed the pattern of their head movement in the presence of a partner during the paired flights compared with during the solo flights (Fig. 6). The birds decreased the rate of head turning during paired flights relative to solo flights (paired t-test, $t_{21}=13.3$, $P<0.001$; Fig. 6C), with decreased saccade frequency ($t_{21}=7.1$, $P<0.001$; Fig. 6D) and saccade amplitude ($t_{21}=13.0$, $P<0.001$; Fig. 6E). These changes were not due to route learning and increasing familiarity with the landscape over consecutive flights because the same patterns emerged when comparing the paired flights with the solo flights conducted after the paired flights (head angular velocity, $t_{21}=13.1$, $P<0.001$; saccade frequency, $t_{21}=10.5$, $P<0.001$; saccade amplitude, $t_{21}=11.2$, $P<0.001$; Table 1). We also examined whether the birds decreased their head movement when they flew across the highways and the railway line during paired flights. In contrast to the patterns found during solo flights, the birds did not show any changes in head movement when crossing these landmarks in pairs (head angular velocity: $\chi^2=2.66$, d.f.=1, $P=0.10$).

Finally, we examined how birds changed the pattern of their head movement during paired flights, in response to the partner's position relative to themselves. Birds in pairs typically flew approximately 5–10 m from each other and rarely at distances greater than 30 m, consistent with previous findings (Pettit et al., 2013). When pairs approached each other closely or flew at distances greater than 5–10 m, this did not change the pattern of their head movement (Fig. S4). Birds in pairs also preferred to fly side-by-side; each bird spent proportionally more time flying alongside the partner than behind or in front of it (paired t-test, $t_{21}=7.15$, $P<0.001$; Fig. 7C), again consistent with previous findings (Pettit et al., 2013). When their partner was located to the side, birds moved their head less overall than they did when the partner was in front or behind ($t_{21}=5.22$, $P<0.001$; Fig. 7G), with decreased saccade frequency ($t_{21}=5.92$, $P<0.001$; Fig. 7H) and saccade amplitude ($t_{21}=3.90$, $P=0.001$; Fig. 7I). Interestingly, the analysis of head orientation revealed that the birds did not change their yaw head orientation
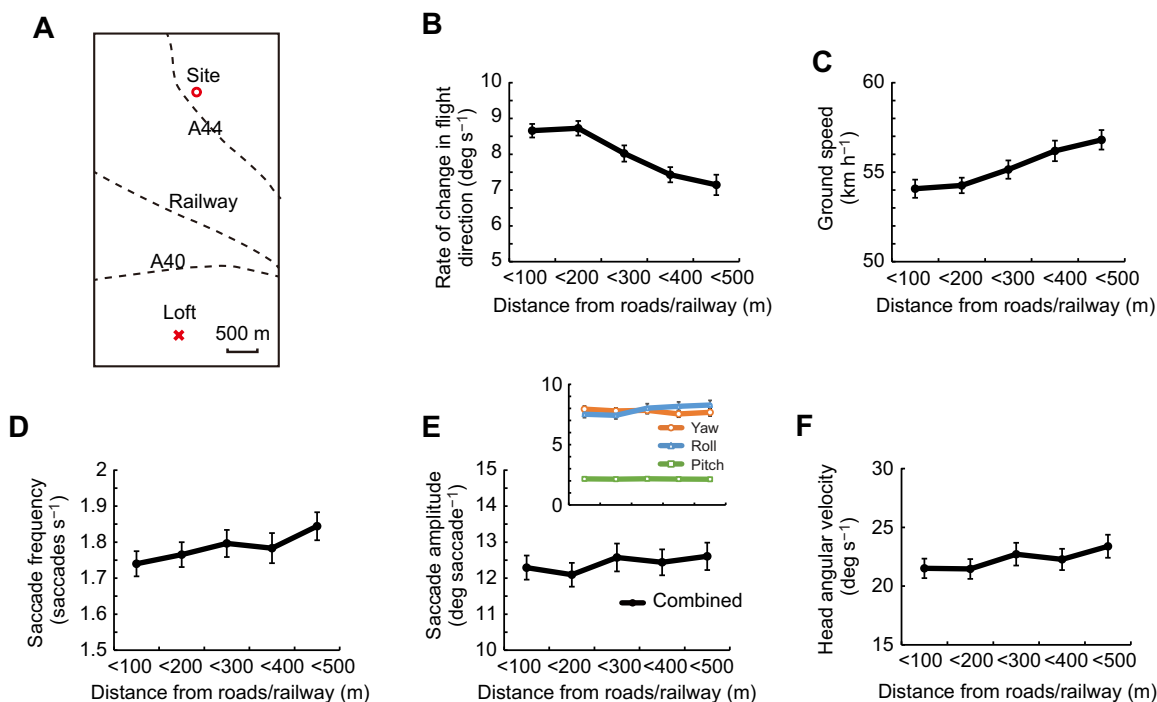
Fig. 5. Changes in head movement and flight patterns as a function of the distance from two major roads and a railway line during solo flights (both before and after crossing). (A) Schematic showing location of roads and railway line on the way to the loft. (B) Rate of change in flight direction (deg s^{-1}). (C) Ground speed (km h^{-1}). (D–F) Head movement characteristics: saccade frequency (D), saccade amplitude (E and inset) and head angular velocity (frequency×amplitude; F). Values are subject means (±s.e.m.) from all 22 birds during solo flights.
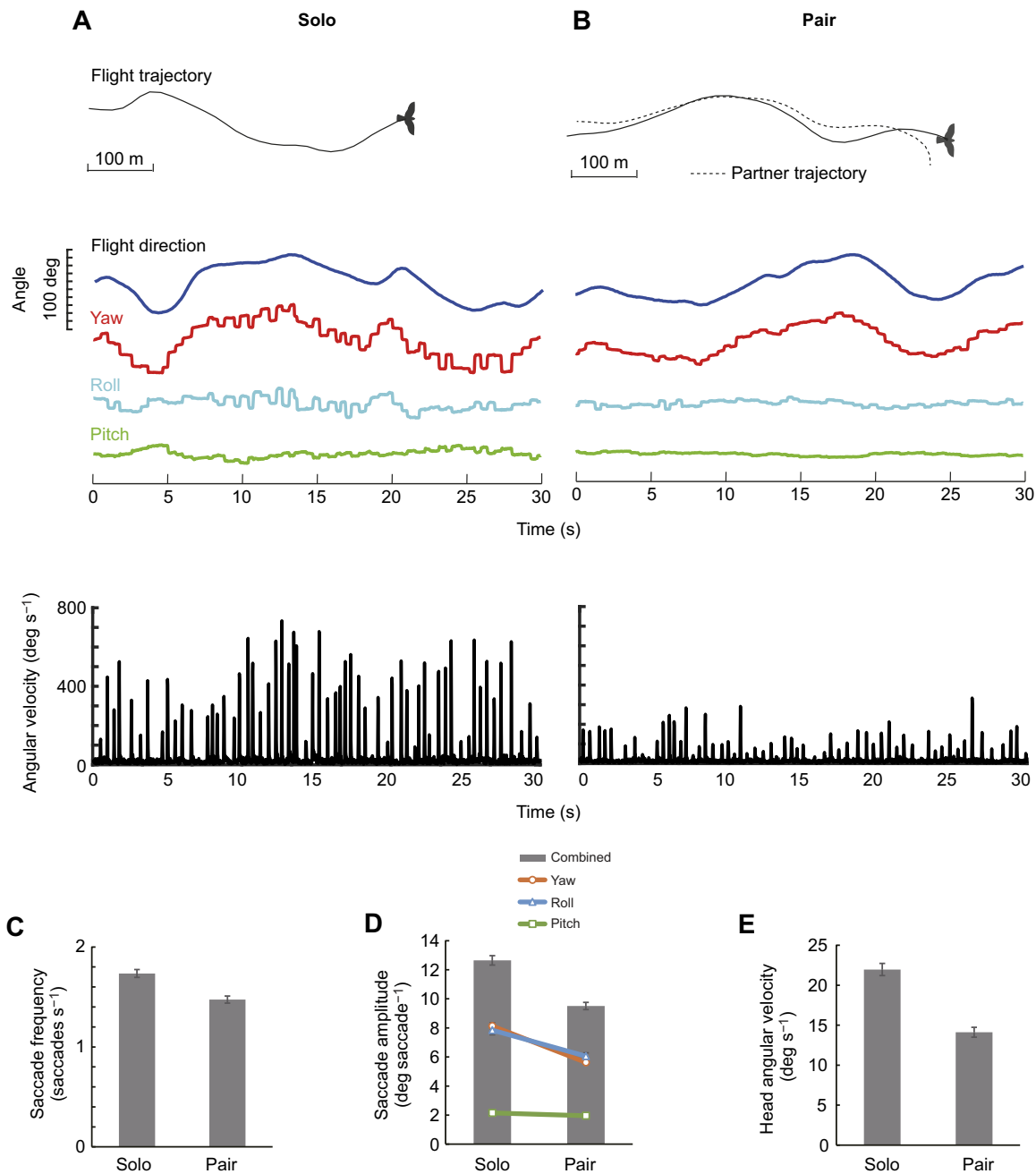
Fig. 6. Head movement in solo versus paired flights. (A,B) Examples of head movement (yaw, roll and pitch angle, and the combined angular velocity) in solo versus paired flights performed by the same bird. (C–E) Head movement characteristics: saccade frequency (C), saccade amplitude (D) and head angular velocity (frequency×amplitude; E). Values are subject means (±s.e.m.) from all 22 birds during the solo and paired flights.

according to their partner's relative position, but instead kept orienting their head direction (or the center of their frontal visual field) towards their flight direction (Fig. S5). These results indicate that the birds decreased their head movement especially when the partner birds were in their lateral vision (at least within 30 m).

It should be noted that these observed changes in head movement were not simply due to potential correlations between head movement and flight turns. As mentioned above, when the birds turned more steeply during flight, they increased their head

movement in the yaw direction but decreased it in the roll direction (Fig. S2). Owing to such offsets, the correlation between the combined head movement and the flight turn was minimal during the solo flights. However, during the paired flights, there was a clear positive correlation between the combined head movement and the flight turn (Fig. S2; this is presumably because the birds decreased their head movement overall when flying straight while they could not do so when turning steeply during the paired flights). Importantly, however, this observed correlation during the paired
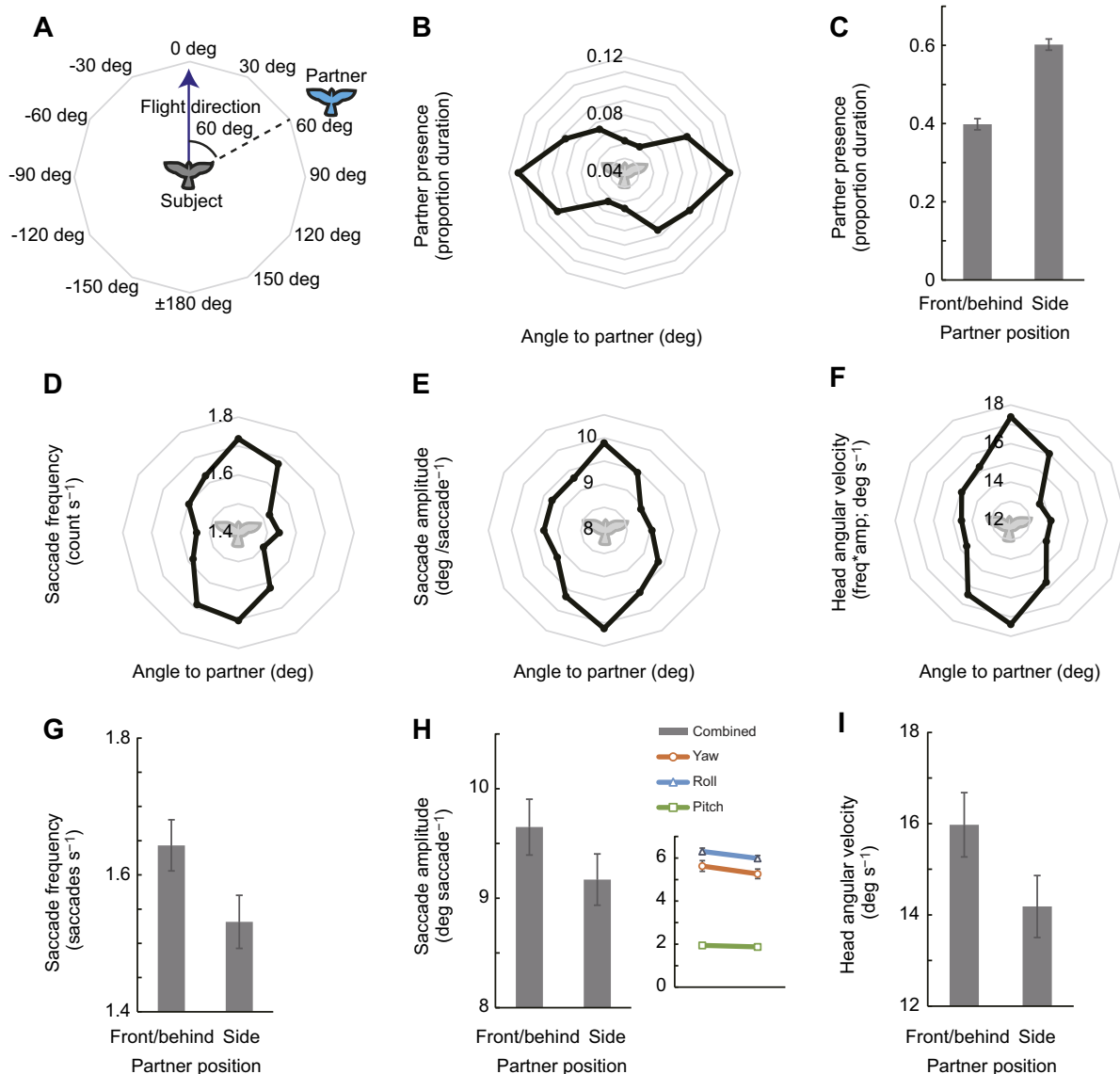
Fig. 7. Saccade properties as a function of the partner's position during paired flights. (A) Angle to the partner (in comparison with the flight direction of the focal bird). (B,C) Likelihood of partner presence (the mean proportion of total flight time when the partner was present). (D–I) Head movement characteristics: saccade frequency (D,G), saccade amplitude (E,H and inset) and head angular velocity (frequency×amplitude; F,I). The bar graphs (C,G,H,I) show the means of the bins in which the partner was flying either in the 'front/back' (−45 to 45 deg and ±135 to ±180 deg) or the 'side' position of the focal birds (±45 to ±135 deg). Values are subject means (±s.e.m.) from all 22 birds during paired flights.

flights could not account for the observed differences in head movement between the solo and paired flights because those differences were observed independently of the rate of changes in flight direction (Fig. S2). Furthermore, the difference in the rate of change in flight direction when the partner was flying alongside versus in front of or behind the bird was small and statistically non-significant (5.47±0.10 versus 5.63±0.12, mean±s.e.m., paired *t*-test, $t_{21}=2.0$, $P=0.06$) and thus could not account for the observed large differences in head movement between those conditions.

DISCUSSION
We successfully obtained high-resolution data on the head movements of homing pigeons completing large-scale

navigational tasks in their natural environment. Our sensor reliably recorded the 3D movement of the head and detected clearly distinctive saccade signals in this movement. Our analysis revealed that birds' head movement has at least three main functions: the stabilization of gaze, the guidance of flight and the scanning of the environment.

Specifically, with regard to the first function, the birds stabilized their head with respect to the environment along all three axes of head rotation (roll, yaw and pitch). This observation is consistent with previous studies that examined pigeons' head movement when they were standing still, walking and flying short distances inside a laboratory setting (e.g. Aldoumani et al., 2016; Eckmeier et al., 2008; Ros and Biewener, 2017; Troje and Frost, 2000; Warrick

et al., 2002). The role of such stabilization is likely the minimization of motion blur (Land, 1999a) and the simplification of motion images experienced while moving, by separating the rotational from translational components of optic flow, particularly during turns (Bhagavatula et al., 2011; Eckmeier et al., 2008; Kress et al., 2015).

Another function of head movement may be the guidance of flight, as the birds adjusted their head orientation during flight maneuvers. We found that the birds turned their head slightly ahead of time in the corresponding direction when the flight trajectories curved, consistent with previous findings obtained in a laboratory setting (Ros and Biewener, 2017). These observations indicate that pigeons tend to orient their head direction toward the immediate goal of their flight path. The purpose of such orientation is likely to take a vantage point from which they can view obstacles approaching them, much like human drivers do (Land and Lee, 1994). Such behavior may also help birds to analyze the steepness of their turns based on the relative speed of the experienced motions in the left and right eye, given that birds use optic flow to guide flight by balancing the speeds of image motions that are experienced in the two eyes during flight (Bhagavatula et al., 2011). Ros and Biewener (2017) pointed out that the consistent angle of the neck relative to the steering direction may allow pigeons to control body and wing movements through cervical feedback.

Importantly, despite the observation that flight maneuvers affected (or constrained) the pattern of head movement to some degree, overall, the birds moved their head far more than necessary for the changes in flight direction. This suggests that they deliberately scanned the environment or actively attended to external visual cues. During such scanning, they moved their head mainly in the roll and yaw directions, and less so in the pitch direction. As such movement of the head allows birds to move their lateral visual fields more widely than their frontal visual fields (compare Fig. 3B and C), our subjects appeared to use mainly their lateral visual field to scan the environment during flight. This is consistent with the idea that pigeons preferentially use their lateral fovea to view distant objects (Dawkins, 2002; Erichsen et al., 1989; Maldonado et al., 1988). Also, it may explain our observation that the birds moved their head much more in the yaw direction (horizontal scan) when they were standing still on the ground compared with when they were flying, presumably to scan the objects at ground level.

During such scanning of the environment, the birds changed the pattern of their head movements in response to prominent visual cues in the environment. For example, we found that head movements decreased when our birds flew across major roads and a railway line. Previous studies have reported that pigeons have strong tendencies to follow linear structures during navigation when these structures run roughly in the direction of home (Biro et al., 2004; Lipp et al., 2004). Previous studies have also reported, and our results confirmed, that birds increase their rate of change in flight direction (i.e. they fly more tortuous paths) and decrease their ground speed near these structures, when they run perpendicular to the direction of home and thus are crossed rather than followed (Guilford et al., 2004; Schiffner and Wiltschko, 2009). This is likely because such prominent edge-type visual landmarks are sources of information within the landscape that aid navigation (Lau et al., 2006; Mann et al., 2014). Therefore, the observed decrease in head movement near linear structures may indicate that the birds changed their focus of attention at such times; either by increasing their attention to those landmarks or by decreasing the search for other landmarks. We did not observe the same changes when birds flew as a pair, perhaps because birds flying together share the navigational

task with each other and this may weaken signatures of individual attention. Our findings echo those of Vyssotski et al. (2009), who showed that flying pigeons show distinct activation of EEG signals when crossing highways. They also found that EEG signals did not change when the birds flew in a flock. Together, these results suggest that flying pigeons visually process and attend to prominent landmarks at the point of decision-making during navigational tasks.

Another clear result was that birds decreased their head movement when they flew with a partner compared with when flying alone. Following on from the observations mentioned above, this finding suggests that the birds changed their focus of attention during paired flight, either because they attended to their partner or because they decreased the search for landmarks or predators. Moreover, we found that the birds decreased their head movement primarily when the partner was flying alongside them rather than in front of or behind them. Together, these results suggest that pigeons are particularly likely to decrease their head movement when they detect partners in their lateral visual field – presumably in the part of the retina they predominantly use during flight.

Two further interesting findings will require additional studies for thorough interpretations, but at present they already provide crucial hints at the way pigeons use their gaze during flight. First, we found that over the course of the first four solo flights from a given release site the birds increased their head movement, and that it was during the same four flights that they established idiosyncratically preferred homing routes (a well-known feature of route learning in pigeons; for a review, see Guilford and Biro, 2014). One speculation based on this result is that birds may modulate their visual scanning behavior during critical learning periods, i.e. as their familiarity with a given terrain increases. That is, during the initial few flights, when familiarity is low, birds may scan more actively for landmarks. Once they have established their own routes, such search/scanning efforts diminish. Interestingly, and largely consistent with the patterns found in this study, a recent experiment examined pigeons' flight speeds and wingbeat characteristics and found a distinct pattern of changes before and after the establishment of preferred routes (Taylor et al., 2017). Together, these results suggest that pigeons may employ distinct sensory and flight strategies depending on their degree of visual familiarity with a landscape. However, it should be noted that our releases were from a relatively close release site (4 km from the loft), and that all subject birds had had previous experience of homing flights. Future tests using the same instrumentation should investigate the role of experience more thoroughly and examine the correlations between learning, head movement and several other parameters of navigation (e.g. point of decision, frequently visited landmarks, visibility of distant landmarks, and altitudes).

Second, the birds did not foveate their partners in that they did not try to hold them at a constant visual angle (Fig. S5). Specifically, they did not change their head yaw orientation according to their partner's location but instead kept orienting their head direction (or the center of their frontal visual field) towards their flight direction (or towards the immediate goals when making turns). One possibility is that pigeons move their eyes but not their head to foveate the partner during paired flights. Yet, this is unlikely given the consistent previous findings that pigeons rarely move their eyes without head movement (at least when they are on the ground; Gioanni, 1988; Haque and Dickman, 2005; Wohlschläger et al., 1993). Thus, they seemed to attend to the partner mainly via their peripheral vision. This is presumably because flying birds need to maintain their head direction in a consistent orientation to analyze

their flight direction. Possibly, as an alternative solution to actively foveating the partner with their head and eyes, birds seemed to instead adjust their position relative to each other, by adjusting their flight speeds and directions (as described in Pettit et al., 2013). Side-by-side configurations in flight may allow the partner to be most readily seen via lateral vision. However, it remains unclear whether flying birds foveate the partners at least occasionally. To answer such questions, the measurement of the gaze targets in the bird's simulated retina are necessary. As a last note, however, one limitation of our current system is the difficulty of conducting such precise measurements owing to the instability of determining absolute orientations in the IMU sensor (see Materials and Methods) and the known inaccuracies of determining longitudes/latitudes in the GPS system. Instead of the IMU–GPS system, a lightweight, head-mounted, wide-angle camera may be a good alternative in future studies because it can capture short-lasting events or stimuli directly in the video images and may thus allow us to further narrow down the birds' focus of attention.

To conclude, despite the above limitation, our pSensor could reliably record pigeons' head movement. The results revealed systematic changes in the pattern of the birds' head movement during large-scale navigation, indicating that the birds changed their gaze strategy in a task-related manner. Tracking birds' head gaze as they freely traverse natural landscapes can thus reveal how they visually attend to the environment during navigation, both individually and in groups.

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