

HEAD-BOBBING IN PIGEONS: HOW STABLE IS THE HOLD PHASE?

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Accepted 17 December 1999; published on WWW 10 February 2000

Summary

The head movement of a walking pigeon *Columba livia* is characterized by two alternating phases, a thrust phase and a hold phase. While the head is rapidly thrust forward during the thrust phase, it has been shown repeatedly that it remains virtually motionless with respect to translation along a horizontal axis (roll axis) during the hold phase. It has been shown that the stabilization during the hold phase is under visual control. This has led to the view that the pigeon's head-bobbing is an optokinetic response to stabilize the retinal image during the hold phase. However, it has never been shown explicitly that the head is really

held stable in space with respect to other translatory or rotatory dimensions. Using videography, we show here that this is in fact the case: except for a small but systematic slip that presumably serves as an error signal for retinal image stabilization, the head of the pigeon remains locked in space not only with respect to the horizontal (roll) axis but also with respect to vertical translation (along the yaw axis) and with respect to rotation around the pitch and yaw axes.

Key words: pigeon, *Columba livia*, head-bobbing, walking, optokinesis, central pattern generator.

Introduction

Like many other birds, pigeons show a very characteristic motion pattern during walking, running and landing flight: the head appears to move rhythmically forwards and backwards. This impression is particularly compelling during walking at slow and moderate speeds. Dunlap and Mowrer (1930) were the first to demonstrate that this impression is illusory. Although the head does move forwards and backwards with respect to the body, this is not the case with respect to allocentric coordinates (i.e. in world coordinates). Instead, the head is held locked in space during a so-called hold phase and thrust forwards during the thrust phase, as has been confirmed by several other authors (Davies and Green, 1988; Friedman, 1975; Frost, 1978; Whiteside, 1931). Hold and thrust phases also seem to occur during pecking (Goodale, 1983; Ostheim, 1997; Zeigler et al., 1993).

Head-bobbing by walking pigeons is synchronized with the movement of the feet (Cracraft, 1971; Daanje, 1951; Dagg, 1977a,b; Dunlap and Mowrer, 1930; Troje and Frost, 1998) and thus has a frequency of approximately 3–8 Hz depending on the speed of the walking bird. At velocities above 70 cm s^{-1} , the hold phase no longer occurs and is replaced by a flexion phase (Davies and Green, 1988; Green et al., 1994) during which the head continues to move forwards in allocentric coordinates while moving backwards with respect to the body. Up to this critical speed, however, the bird seems to hold its head motionless in space while the body continues travelling at a relatively constant velocity.

The synchronization of head-bobbing with the movements

of the feet is suggestive of a purely biomechanical function, comparable with the swinging of the arms of walking humans (Dagg, 1977b). However, there is plenty of evidence that head-bobbing serves a visual function. In a series of experiments, Friedman (1975) showed convincingly that head movements in the pigeon are controlled by visual rather than vestibular or biomechanical stimulation. Frost (1978) confirmed this view by letting pigeons walk on a treadmill. If the bird's walking speed matched the belt velocity, no head-bobbing was observed. However, if the bird was moved passively, head-bobbing occurred even without accompanying walking movements.

These findings suggest that head-bobbing should be regarded as an optokinetic response similar to optokinetic eye movements in humans and many other animals (Wallman and Letelier, 1993). At least one of its functions seems to be to stabilize the retinal image during the hold phase. The thrust phase is needed for the head to catch up with the body, which is constantly moving forwards. In addition, further visual functions of the thrust phase have been proposed, in particular, gaining depth information from motion parallax. This idea is particularly attractive in view of the fact that head-bobbing also occurs during running and landing flights at velocities that no longer allow head stabilization during the hold phase.

To date, all measurements concerned with the head-bobbing of walking pigeons have recorded only the horizontal component of the trajectory of the pigeon's head in the sagittal plane. This component is certainly the most prominent for a

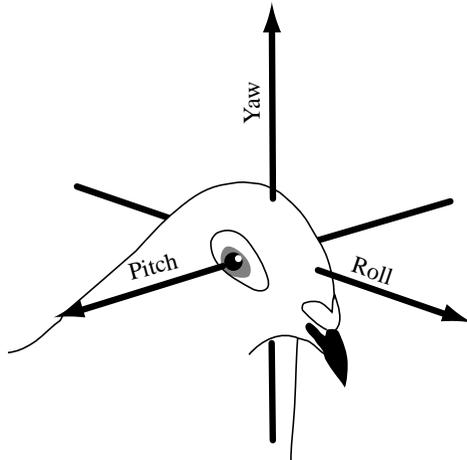


Fig. 1. The three axes that define the motion of a pigeon's head in space. The head can either move along an axis or rotate around an axis.

pigeon simply walking along a straight line. However, it represents only one of six different components needed to describe a movement in three-dimensional space: there are three translational and three rotational components. These components can be addressed by means of the three axes of rotation: the pitch axis, the yaw axis and the roll axis around which the head can be rotated or along which it can be translated (Fig. 1).

Although translation along the roll axis is most salient in normal straight walking, most of the other movement components can become very prominent during more complex behaviours. Rotational components (yaw) come into play during turning, and vertical translation and pitch rotation become very salient during the expressive bowing behaviour that forms part of the complex courtship display. If the primary function of the hold phase is to stabilize the retinal image by locking the head in space, then this stabilization should be observed not only in translational movement along the roll axis but also for all other components.

To test this hypothesis explicitly, we recorded the motion of a pigeon's head in a behavioural context that included both pronounced translational motion along the roll and yaw axes and rotational motion around the pitch and yaw axes. The data were then parsed automatically into hold and thrust phases, which were defined only on the basis of the horizontal component. We then quantified the degree of motion for the other motion components and compared motion during the hold and thrust phases.

Materials and methods

Experimental arrangement

Two different groups of five pigeons (*Columba livia* L.) each served as subjects for the collection of motion data. The first group were all male birds videotaped while displaying courtship behaviour that contained pronounced vertical head movements or 'bowing'. Prior to the experiment, the birds had

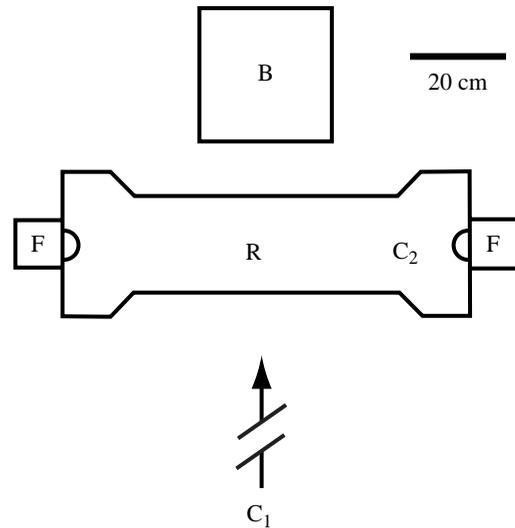


Fig. 2. Schematic diagram of the runway (R) as seen from above. A food hopper (F) is mounted at each end of the runway. An infrared light-barrier system detects when the pigeon picks up a seed and triggers food delivery at the other end of the runway. The food hoppers were only active when recording the top-view footage. They were inactivated and covered when collecting data from courting birds when a receptive female bird placed in a Plexiglas box (B) was visible to the male bird. The camera position was either 340 cm away at the same height as the pigeon, capturing it in profile view (C_1), or 150 cm above the right food hopper, viewing the pigeon in top view (C_2).

been sexually deprived by keeping them in individual cages for at least 1 week. During this time, they were allowed to become accustomed to the Plexiglas runway by letting them explore it for 10 min per day. Only one bird was allowed in the runway at a time. The runway contained a narrow central region that made turning movements difficult. It thus encouraged linear motion in this region and allowed comfortable turning only at the two ends (Fig. 2). The purpose of the runway was to restrict movement in the central part so that it occurred only in the image plane of a video camera placed 340 cm away from the runway at the same height as the pigeon, thus showing the bird in profile view while walking through the narrow part of the runway.

During the experimental sessions, the birds were shown a receptive female bird placed in a Plexiglas container next to the runway. The two birds could not make physical contact but could readily see and hear each other. Both birds displayed their typical courtship behaviour, although the path of the males, which normally walk around in circles and figures-of-eight if space is unconstrained, was now restricted to straight walking in the central region of the runway and turning at its ends.

The second group consisted of birds videotaped from above during turning movements in the same runway. Before the experiment, they had been trained to walk back and forth between two food hoppers mounted at the two ends of the runway. Each hopper was equipped with a light barrier that

registered when a bird picked up a millet seed that was offered in the hopper. The signal from the light barrier was used to trigger the hopper at the other end of the runway to deliver the next seed. The birds quickly learned to move back and forth between the feeders. No other bird was present during experimental sessions. The video camera was mounted 1.5 m above one end of the runway and recorded the turning motion subsequent to picking up a seed and before walking back to the other end of the runway from a top-view perspective.

Data collection

We recorded 10 sequences from each bird. The material consisted of 50 straight courtship runs and 50 turning movements. A digital video camera (Sony DCR-VX1000) was used for recording at 30 frames s⁻¹ (i.e. 60 fields s⁻¹), and a capturing board (Pinnacle Miro DV300) was used to stream the footage to a computer hard drive. Custom-designed software was developed to record the image coordinates of feature points (see below) on the pigeon’s head in each single video field. The image coordinates of two calibration points on the runway were also measured and used to translate the image coordinates into real-world distances. This calibration is accurate for the profile-view data because of the large camera distance used (and the corresponding small viewing angle), but less reliable for the top-view data because of larger perspective distortions due to the shorter camera distance. The spatial resolution of the system in both cases was approximately 1 mm, and the sampling frequency was 60 Hz.

The feature points in the footage taken from the courting males in profile view were the eye and the tip of the beak. The data used for further evaluation were the position of the eye along the roll and yaw axes (corresponding, respectively, to the horizontal and vertical coordinate in the image plane) and the orientation of the eye around the pitch axis. The feature points tracked in the top-view footage were the tip of the beak and a point exactly mid-way between the two eyes. The derived data that were used for further evaluation were the path length travelled by the mid-eye point and the yaw angle. The path length *l* was computed from the *x* and *y* image coordinates according to:

$$l(t_i) = \sum \sqrt{\Delta x_i^2 + \Delta y_i^2}, \tag{1}$$

where *t* is time and *i* is the number of the image. Fig. 3 shows examples of both profile-view and top-view data and also depicts their subsequent analysis.

Data analysis

For further analysis, the motion data were parsed into hold and thrust phases. This parsing was done using the horizontal positional data *x* of the eye for the profile-view footage and the path length *l* for the top-view footage. The temporal structure of the hold phases was detected in two steps by first roughly determining where hold phases occurred and then using a robust estimation technique (Rousseeuw and Leroy, 1987) to fit a line function to the data around this point.

For the first step, the data were heavily smoothed and local minima of the first derivative were calculated, yielding a series of time values (one for each hold phase) that were somewhere in the middle of a hold phase. Each single time value, together with its respective positional value, then defined a constant function that was used as a starting point for a robust regression fit.

For this second step, a Gauss–Newton algorithm was used to find the local minimum of

$$e = \sum \frac{h^2}{\sigma^2 + h^2}, \tag{2}$$

where $h=(d-m)^2$, *d* stands for the data (the time series of horizontal positions) and $m=ax+b$ stands for the regression line to be fitted. In contrast to a least-square fit, the robust fit is not affected by outliers. The value of σ defines what an outlier is meant to be. Data values for which $h>\sigma^2/3$ have a strongly reduced influence on the solution and can be viewed as outliers. We used a value of $\sigma=1$ throughout this study, resulting in very conservative fits. The hold phase was then defined as the time between the first and last time value for which *h* was smaller than $\sigma^2/3$.

To determine the degree of head motion during hold and thrust phases, the standard deviation of the positions and orientations during each hold and each thrust phase was calculated.

Results

Mean head-bobbing frequency was 3.46 Hz for the courting birds (profile-view footage) and 4.25 Hz during turning behaviour (top-view footage). The hold phase represented 54% and 59% of the overall time for profile-view and top-view data, respectively. The mean durations of the hold phase were therefore 156 ms and 139 ms, respectively, and the mean durations of the thrust phase were 132 ms and 96 ms, respectively.

Table 1 presents results on the amount of head motion during the hold and thrust phase in terms of the mean standard deviation of positional and orientational variables. The variation within the hold phase is negligible for the horizontal position in the profile view and for the path length in the top view as a direct consequence of the way that the hold and thrust phases were defined. However, the positional variation along the yaw axis is not much larger during the hold phase, and the

Table 1. Mean standard deviation of positional and orientational data within hold and thrust phases

	Hold phase	Thrust phase
Position along roll axis, <i>x</i> (mm)	0.34	27.60
Position along yaw axis, <i>y</i> (mm)	0.94	9.01
Rotation around pitch axis (degrees)	0.97	5.20
Position along the path, <i>l</i> (mm)	0.70	25.13
Rotation around yaw axis (degrees)	0.61	6.20

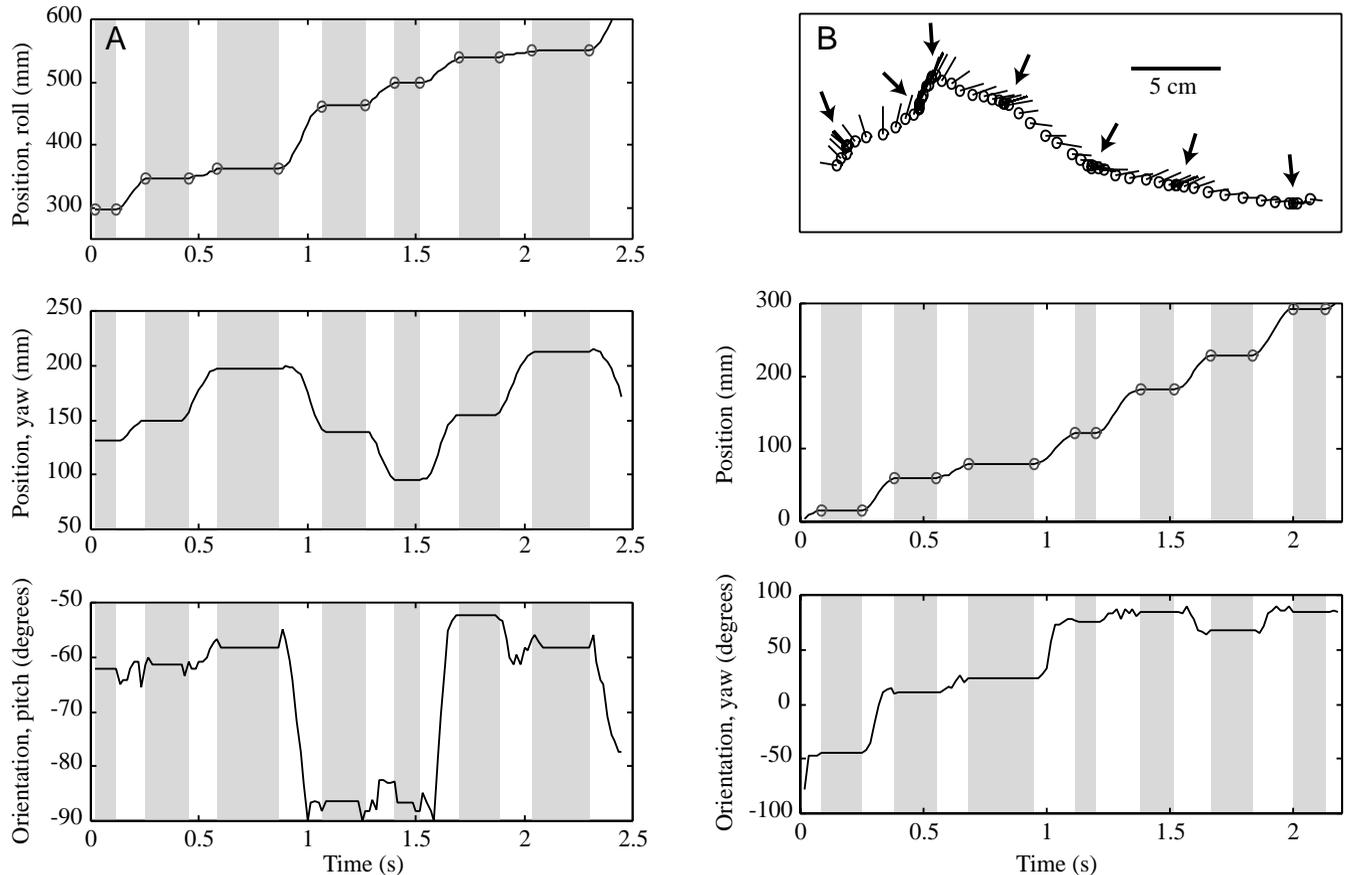


Fig. 3. (A) Positional and orientational data derived from the profile-view footage of a pigeon. In the upper diagram, the horizontal position of the eye (position along the roll axis) is plotted against time. The circles and the shading mark the beginning and end of the hold phases defined as described in the text. The two lower diagrams show vertical position (position along yaw axis) and pitch, respectively. The shading in the upper diagram is repeated in the lower panels to illustrate where hold and thrust phases occur. (B) Positional and orientational data derived from the top-view footage of a pigeon. The upper panel shows the position and orientation of the head in the runway. Circles represent the mid-eye location, and the ends of the lines correspond to the position of the tip of the beak. Arrows mark where hold phases occurred. The middle diagram shows the path length travelled plotted against time. Circles and shading mark the hold phases. The lower diagram shows the orientation of the head around the vertical axis. The shading is repeated from the middle diagram.

orientational variations during the hold phase are also very small. All values increase considerably during the thrust phase.

Interestingly, the small variation in position during the hold phase can be explained to a great extent by a small but consistent positional slip during the hold phase. The slope of the line m fitted to the data (see equation 2) deviates slightly but systematically from zero (sign test, $P < 0.001$). The mean slope calculated over all hold phases in the profile-view data is 3.15 mm s^{-1} with a standard deviation of 2.9 mm s^{-1} . The mean slope fitted to the top-view data is with 6.17 mm s^{-1} with a somewhat higher standard deviation of 3.7 mm s^{-1} . The mean r^2 value, which accounts for the ratio of the overall variance that is covered by the fitted model, is 0.53 for the profile-view data and 0.72 for the top-view data, very large values considering the small slopes (note, that r^2 for a linear fit with zero slope is zero in any case). To investigate further whether the slope of the fitted line results from a systematic deviation of the data from a straight line at the beginning and the end of the hold phase, we performed a similar calculation using only

the central two-thirds and finally only the central one-third of the data of each hold phase. Even in the latter case, a sign test yielded significant evidence ($P < 0.01$) for a positive slope.

These very shallow slopes definitely challenge the spatial resolution of our data-acquisition system and, consequently, we do not have complete confidence in the values obtained. The magnitude of the slip is probably also dependent on the distance from the bird of the objects in the visual environment of the bird that contribute to the optic flow field, a variable that was particularly well controlled in the present experiments. The fact, however, that there is a slope larger than zero during the hold phase can be confirmed statistically with high significance (sign test, $P < 0.001$).

Discussion

Except for a small slip, the pigeon's head is stabilized in space not only with respect to horizontal translation along the roll axis but also with respect to vertical translation and

rotations around the pitch and yaw axes. We did not measure lateral translation (along the pitch axis) and rotation around the roll axis explicitly; however, the occurrence of both seems to be very unlikely during the hold phase, and we found it impossible to devise a behavioural context in which we would expect these movement components to occur during the thrust phase. Our data thus confirm the view that the hold phase of the pigeon's walking cycle serves in retinal image stabilization, possibly to facilitate image processing and in particular the detection of moving objects.

In their original study on head-bobbing, Dunlap and Mowrer (1930) suggested that the existence of a slight slip of the head's position during the hold phase might provide the necessary error signal that drives the compensation mechanism. After ruling out the possibility that kinesthetic cues could provide the error signal, they wrote (p. 105): 'A somewhat dubious alternate explanation is, that the head is not actually at rest,... but is moving forward very slightly, just enough to produce sufficient change in the bird's visual field to prompt the compensatory effect.' However, with the technique used, they were not able to measure any such slip. Frost (1978) anecdotally reported an accidental observation that he interpreted to reflect the predicted slip: a pigeon that was still standing on the treadmill he had used for his experiments slowly assumed a strange posture by stretching its neck farther and farther ahead until it lost equilibrium and eventually toppled over. Inspecting the equipment, he found that the treadmill had not been turned off completely, as intended, but was still moving at a very slow imperceptible (to the experimenter) speed. Apparently, the belt velocity was too slow to induce walking but still triggered compensatory head movements. From the little footage that Frost (1978) managed to record of this 'extended hold phase', he measured a slippage of the head's position of approximately 3.6 mm s^{-1} , a value approximately the same as that we measured in the present experiment.

The magnitude of the retinal slip during the hold phase also matches electrophysiological data from the nucleus of the basal optic root (nBOR), the major nucleus of the accessory optic system (AOS) of the pigeon. The AOS is considered to play a major role in the stabilization of the retinal image (Simpson, 1984; Westheimer and Blair, 1974). Morgan and Frost (1981) and later Wylie and Frost (1990a,b) showed that nBOR cells respond to large flow fields with velocities as small as 0.5° s^{-1} . A textured background at a distance of 40 cm (approximately the distance at which the dorsal retina would see the floor) would induce a flow field of 0.5° s^{-1} when the pigeon's head moves with a slip velocity of 3.5 mm s^{-1} .

In conclusion, the present study demonstrates that the head of walking pigeons is stabilized with respect to both translatory and rotatory movement. Moreover, the results show that, conversely, all other movements are synchronized with the saccadic-like forward thrust of the head. This synchronization adds to a general pattern of synchronization that also involves the movement of the feet during walking (Dagg, 1977b), of the wing beat during landing flight (Davies and Green, 1988;

Green et al., 1994) and even of the head movements during pecking (Goodale, 1983). Lemeignan et al. (1992) demonstrated that, although pigeons can move their eyes independently with respect to viewing direction, saccades in each eye always occur synchronously. Furthermore, eye movements seem to occur only during thrust phases (Pratt, 1982).

Collectively, this suggests that a central pattern generator must be involved in the coordination of this complex pattern of motion output, which may also be involved in gating input from the accessory optic system during saccadic reorientations of the head. It has been shown recently (Galubitski et al., 1998, 1999) that the whole set of complex quadrupedal gaits can be generated by a single central pattern generator architecture, and these authors pointed out that this has enormous evolutionary advantages. The pigeon data seem to support this view and even extend it. The same central pattern generator might be used not only for different gaits in the same animal but even for different kinds of locomotion (walking, flight) and other behaviours (e.g. pecking).

Alexandra Hernandez did an excellent job helping to videotape the pigeons. She also did the very work-intensive manual digitization necessary to acquire the motion data with great patience. Our research assistant Sharon David was the major organizing force in the laboratory and helped skilfully on many aspects of the project. This work was partly supported by an NSERC grant to B.J.F. and by a fellowship of the Alexander-von-Humboldt Foundation to N.F.T.

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