J Comp Physiol A (1994) 174:249–256

Journal of Comparative Physiology A Sensory, Neural, and Behavioral Physiology

Head-bobbing and head orientation during landing flights of pigeons

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Accepted: 23 August 1993

Abstract. 1. The head-bobbing rhythm previously reported in pigeons *Columba livia* during approximately level landing flights also occurs in upwards landing flights. This finding strengthens the evidence that head-bobbing in flight is linked specifically to approach to a landing target, and that the behaviour has a visual function.

2. In both level and upwards flights, head-bobbing arises from an oscillating flexion and extension of the neck. Rhythms in translation and rotation of the body do not make a detectable contribution to head-bobbing.

3. Head-bobbing occurs at the same frequency as the wingbeat cycle and in a fixed phase relationship to it.

4. The orientation of the head relative to the horizontal is correlated with the trajectory of upwards approach to a perch. In contrast to downwards landing flights, this relationship cannot have the function of keeping the perch in focus during landing. It is proposed instead that it enables the head to be bobbed along the axis which maximizes amplification of optic flow.

Introduction

In order to alight from flight, a bird must rapidly perform a complex sequence of actions. The posture of the wings and tail must be adjusted in order to brake, the feet must be extended to make accurate contact with the perch, and a stable perching posture must be achieved once contact is made. The visuomotor control of these actions is not yet understood, but two reports have shown that control of the movement and position of the head plays a part in the overall organization of landing.

Davies and Green (1988, 1990) found that pigeons move their heads rhythmically backwards and forwards relative to the body during landing flight, with a frequency of about 10 Hz. This 'head-bobbing' is similar to that seen in walking pigeons (Davies and Green 1988; Dunlap and Mowrer 1930; Friedman 1975; Frost 1978), although there is one important difference. During walking, the head-bob cycle consists of a 'hold' phase, in which the head is stabilized relative to the surroundings, and a 'thrust' phase, in which it moves rapidly forward. During landing flight, however, there is no hold phase in which the head is stabilized, and instead the forward velocity of the head oscillates in an approximately sinusoidal manner, with a 'flexion' phase following each thrust phase. This sinusoidal pattern can also be seen when pigeons run at speeds greater than 75 cm/s (Davies and Green 1988).

Pigeons do not head-bob when taking off from the ground (Davies and Green 1988), suggesting that the behaviour is not a mechanical or reflex consequence of the 'clap-fling' wingbeat used in slow flight (Aulie 1983). The implication is instead that head-bobbing in flight is associated specifically with approach to a landing target and has some visual function. Similarly, evidence for a visual function of head-bobbing during walking is provided by the findings that pigeons head-bob when carried passively through space (Dunlap and Mowrer 1930) and that head-bobbing does not occur during walking if image motion is prevented (Friedman 1975). Two possible visual functions during walking have been suggested (Frost 1978). Stabilization of the retinal image during the hold phase may enhance motion or pattern detection, or increased head velocity during the thrust phase may increase the accuracy with which spatial information can be obtained from optic flow.

The fact that head-bobbing occurs in fast running and in landing flight, without stabilizing the retinal image, suggests strongly that the behaviour has some other function besides the enhancement of motion and pattern detection, although the lower image velocity in the flexion phase of the cycle could be significant for these visual functions. It is therefore likely that head-bobbing during landing flight plays a role in maximizing the information which can be obtained from optic flow about the location and structure of the perch (Davies and Green 1988; Lee et al. 1993).

As well as bobbing their heads during landing flight, pigeons adopt a head posture which is closely linked to

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their approach trajectory. Erichsen et al. (1989) showed that the angle between the horizontal and the line joining the centre of the pupil of a pigeon's eye to its beak tip is maintained at approximately 35° during level flight, walking, perching and standing, but that the angle increases during landing flight. Green et al. (1992) confirmed this observation and also showed that a specific relationship holds between head orientation and landing trajectory. As the bird's trajectory becomes steeper, there is a linear increase in the angle of the head relative to the horizontal.

This relationship between trajectory and head orientation has the effect of keeping the position of the perch in the visual field between 20° and 25° above the beak until the eye is about 50 cm from the perch. This position in the visual field does not correspond to any anatomically distinct retinal area, although it does correspond to the elevation where overlap between the visual fields of the two eyes is greatest (Martin and Young 1983). However, the gain in binocular overlap achieved by altering head orientation is relatively small. A further functional explanation considered by Green et al. (1992) was that head posture keeps the perch in focus throughout landing without the need for accommodation.

There is evidence that pigeons are myopic in the lower visual field, and that the myopia increases with increasing elevation below the horizontal, according to a sinusoidal relationship (Fitzke et al. 1985; Hodos and Erichsen 1990). This relationship is such that, if the bird stands at normal height with its head held at 35° to the horizontal, all points on a level ground surface will be in focus simultaneously. If flying horizontally towards a perch at the appropriate distance below the flight path, the perch will lie in the plane on which all points are in focus. In the case of downwards flight, the plane must be tilted through the same angle as that between the flight path and the horizontal, and this can be achieved by turning the head downwards by that angle. Green et al.'s (1992) results match this prediction closely.

The aims of the present experiments are to extend the earlier observations of head movement and orientation in 3 ways. First, Experiment 1 is intended to provide additional information about the kinematic basis of head-bobbing during approximately level landing flights, through a more thorough analysis of body, head and wing movement. Davies and Green (1988) have shown that the rhythm in head velocity in such landing flights does not arise from a rhythm in the path velocity of the body; rather, body velocity regularly shows a low amplitude rhythm in antiphase to that of the head. The source of the head-bobbing rhythm could therefore be either in alternating flexion and extension of the neck, or in oscillating rotation of the body in the sagittal plane around a point near the shoulder, or in a combination of the two. In order to test these possibilities, measures of the angle of attack of the body during landing flight, and of flexion in the system of cervical joints, were obtained.

Experiment 1 also examines the relationship between the head-bobbing rhythm and the wing-beat cycle. If head-bobbing arises from oscillating rotation of the body in flight, a close relationship with the wing-beat cycle would be expected. Alternatively, if it arises from flexion and extension of the neck, a relationship with the wing-beat cycle would indicate that the two motor systems were driven by a single control system.

Experiment 2 repeats this analysis for landing flights in which pigeons fly on a steep upwards trajectory towards a perch. It is important to determine whether head-bobbing occurs in these flights, because Davies and Green's (1988) comparison of upwards take-off flights into open air with level flights towards a perch does not provide fully satisfactory evidence that head-bobbing is associated with landing, rather than being a mechanical effect of slow flapping flight. It is possible that the different forces arising during wingbeat in level and in upwards flight could be the cause of the observed difference in head motion. However, if head-bobbing is observed in upwards flights towards a perch, it can be safely concluded that the behaviour occurs specifically during approach to a landing target, and is not a mechanical consequence of flight activity.

In Experiment 3, the angle at which birds' heads are held relative to the horizontal is measured during upwards landing flights. Green et al. (1992) found that, during downwards landing flights over a range of trajectories from 0° to 30°, this angle is greater than during perching. Does the head turn in the opposite direction during upwards landings and, if so, does its orientation show the same relationship with trajectory? If it does not, the implication would be that different visuomotor organization is involved in downwards and in upwards landing flight.

Experiment 1

Materials and methods

Five birds were used, drawn from a colony of homing pigeons (*Columba livia*) consisting of individuals of both sexes and of ages from one year upwards. Their flight behaviour was recorded in a flight cage 5.47 m long, 0.87 m wide and 2.04 m high, while flying towards a cylindrical perch 75 cm long and 2 cm in diameter fixed transversely across the cage. The starting point and perch were at about the same height and were 3.3 m apart. All the birds were familiar with the flight cage and with the procedure of being filmed while making landing flights. The rear wall of the cage was covered with a white screen with horizontal calibration lines.

Each bird made 4 flights, and was filmed in natural daylight using a Panasonic MV7 solid state video camera, with an electronic shutter providing an exposure time of 1 ms and a field of view extending about 1 m back from the perch. The last flight made by each bird was analyzed, using a frame grabber to store the individual video fields making up the flight, beginning with the first field in which the bird's head was visible and ending with the field in which the feet first contacted the perch. Each landing yielded between 20 and 26 video fields, 20 ms apart, depending upon the angle and speed of the landing approach. These fields were then displayed on a monitor screen and electronically superimposed cross-hairs were used to obtain the X and Y co-ordinates of (i) the centre of the pupil of the eye, (ii) the point on the breast where the sternum protruded furthest, (iii) the shoulder joint, (iv) the tip of the wing and (v) the base of the tail.

The co-ordinates obtained from the video fields were then used to calculate the following parameters (accuracies of each measurement, expressed as ranges from a sample of repeated measurements,

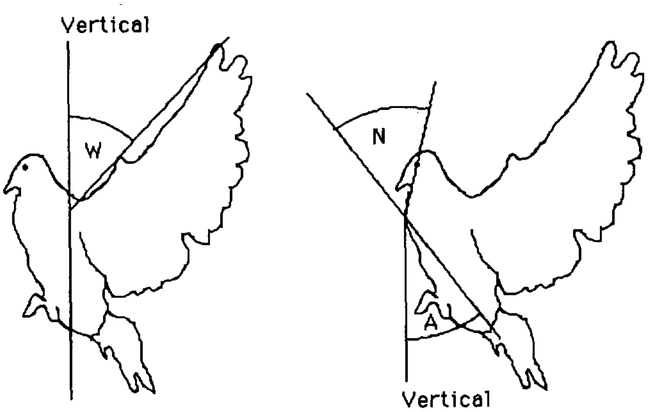

Fig. 1. *W* 'wing angle', between the vertical and the line joining the shoulder and the wingtip. *A* 'angle of attack', between the vertical and the line joining the shoulder and the base of the tail. *N* 'neck angle', between the shoulder-base of tail line and the line joining the shoulder and the centre of the eye. In this illustration, W is negative and A and N positive

are given in brackets): (i) The path velocity of the eye (±11 cm/s), estimated from the distance travelled by the centre of the pupil of the eye between successive fields. (ii) The path velocity, and horizontal and vertical components of velocity, of the body (±11 cm/s), estimated from the distance travelled by the breast point between successive fields. (iii) The 'wing angle', between the vertical and the line passing through the shoulder joint and the wing tip, positive when the wing tip is forward of the body (±1.1°). (iv) The 'angle of attack' of the body, between the vertical and the line passing through the breast point and the base of the tail, positive when the body is tilted forwards (±1°). (v) The 'neck angle', between the line passing through the breast point and the base of the tail, and that passing through the breast point and the centre of the pupil of the eye, positive when the eye is behind the breast point-base of tail line (±1.8°). The three angular measurements are illustrated in Fig. 1.

Since the wing is raised above eye level and obscures the head once during each wingbeat cycle (Davies and Green 1988; Erichsen et al. 1989), the position of the eye or breast could not be recorded in some fields. In these cases, parameters were estimated from interpolated positions of eye and breast midway between those in adjacent fields. Note that this is a conservative procedure, which will tend to smooth out fluctuations in velocity.

Results

Data from two of the 5 landing flights are shown in Fig. 2. The results for body and head path velocity, and the difference between them, are closely similar to those obtained by Davies and Green (1988). Head velocity shows a stochastic rhythm with a period of 120–140 ms (±10 ms), which is only apparent in body velocity as a rhythm of smaller amplitude but in antiphase. The horizontal and vertical components of body velocity also show a relatively smooth time course, and lack any indication of the head velocity rhythm.

The new findings are contained in the 3 angular measurements. To enable direct comparison of these data with the velocity measures above, they are expressed as the *change* in each angle over the 20 ms interval between fields. Change in wing angle shows a clear relationship with head velocity. Both show a rhythm with the same period, and the thrust phase of the head-bobbing cycle coincides with the phase of the wingbeat cycle in which the wing tip travels forwards and then back again between the midline and its furthest forward position. The slow phase of the head-bobbing cycle occurs while the wing is behind the midline.

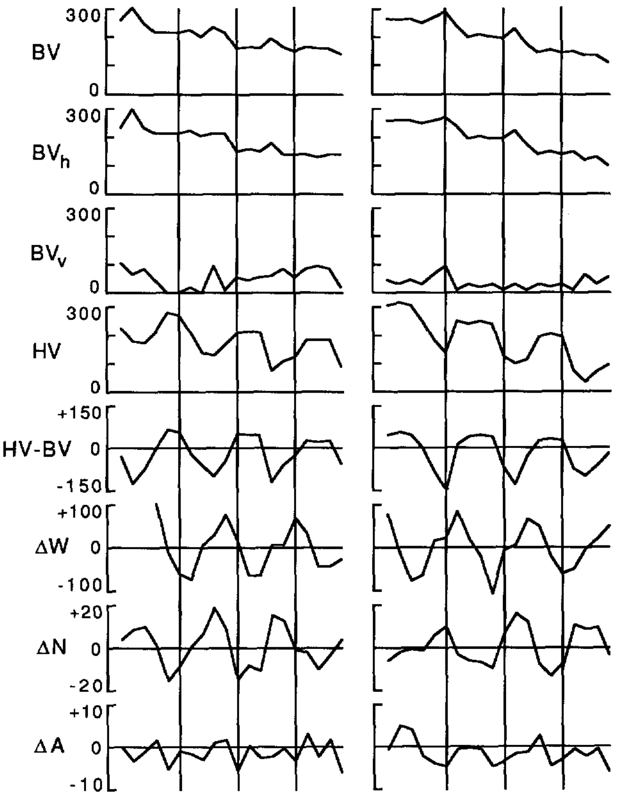

Fig. 2. Data from two approximately level landing flights. *BV* body path velocity; BV_h, BV_v horizontal and vertical components of body velocity; *HV* head path velocity; *HV–BV* head path velocity minus body path velocity; Δ*W* change in wing angle between successive fields (positive values indicate that the wing tip is travelling forwards); Δ*N* change in neck angle between successive fields (positive values indicate that the head is undergoing flexion); Δ*A* change in angle of attack between successive fields (positive values indicate that the body is pitching forwards). Velocities are measured in cm/s, angles in degrees. Vertical lines are at 100 ms intervals.

If the rhythm in head velocity arises from oscillating rotation of the body during flight, we would expect to see a rhythm in the change of angle of attack. This angle increases as the body pitches forward (see Fig. 1), and so positive values of the change in angle of attack would coincide with the thrust phase of the head-bobbing cycle. There is some indication of such a relationship in the right-hand record in Fig. 2, but none in the left-hand record. In both cases, however, there is a much clearer relationship between neck angle and head-bobbing. If the head moves forwards relative to the body, neck angle decreases (see Fig. 1), and so the decrease in neck angle coinciding with the thrust phase in both records in Fig. 2 demonstrates that the major source of the head-bobbing rhythm is motion of the head relative to the body, caused by flexion and extension of the neck.

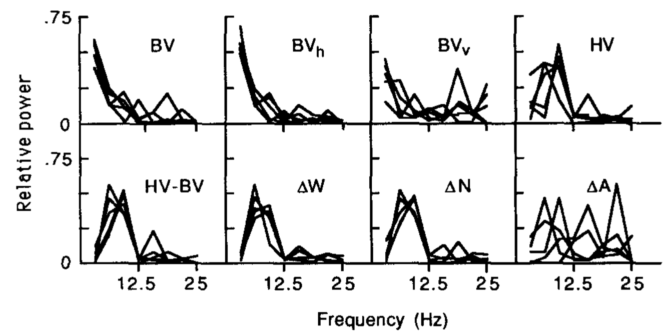

Fig. 3. Frequency domain representation of data from last 340 ms of all five approximately level landing flights. The relative power at each harmonic of the fundamental (3.125 Hz) is shown. Labels as in Fig. 2

Table 1. Test for white noise applied to level and upwards flights

Level flights			Upwards flights		
N	*d*	*P*	*N*	*d*	*P*
20	0.365	NS	20	0.599	<0.01
20	0.629	<0.01	22	0.551	<0.01
24	0.460	<0.01	20	0.232	NS
18	0.588	<0.01	24	0.552	<0.01
24	0.550	<0.01	22	0.465	<0.05

N number of data points in time series. *d* maximum difference between observed and expected cumulative probabilities. *P* level of significance

The consistency of the results from all 5 flights is illustrated in Fig. 3, which shows the Fourier transform of the data from all the records. So that records of differing lengths would be comparable, the last 16 measurements from each flight were used in the transform. For head velocity, head velocity minus body velocity, change in wing angle and change in neck angle, the spectra obtained are closely similar, with peak power in the region 6–9 Hz, while this pattern is absent in the records of body velocity and angle of attack. There is therefore consistent support for the hypothesis that the oscillation in head velocity characteristic of head-bobbing is caused primarily by alternating flexion and extension of the neck, phase-locked to the wingbeat cycle. Periodicities in the translation and rotation of the body do not have the appropriate frequency or phase to account for head-bobbing.

As a further test of the consistency of head-bobbing across all five flights, the significance of the periodicity in head velocity was tested in each one. As autocorrelation methods (Davies and Green 1988) are not fully satisfactory for this purpose, Jenkins and Watts' (1968, p 234) test for white noise was used. Here, the cumulative proportions of the power at each harmonic in the Fourier spectrum are compared to the cumulative probability distribution expected on the null hypothesis that the time series is generated by a white noise source, using the Kolmogorov-Smirnov test. Using all the values for head velocity available, 4 of the 5 records show a periodicity in the head velocity data significant at the 0.05 level (Table 1); the record which failed to reach significance is that on the left of Fig. 2. In light of the consistency in periodicity across records shown in Figs. 2 and 3, this anomaly can be attributed to the use of shorter time series than those used by Davies and Green (1988).

Experiment 2

Material and methods

In order to record upwards landing flights, a perch was fixed transversely across the flight cage just in front of a hatchway providing access to the aviary containing nesting boxes, located in one end wall of the flight cage. This perch was 1.1 m above the ground, 0.74 m wide and rectangular in cross-section with dimensions 32 mm high and 13 mm wide. Pigeons were gently prompted to walk along the floor of the cage until they were between 2.5 m and 0.5 m from the end wall containing the hatchway and approximately midway across the cage, when they were startled by a handclap. Their response was to fly upwards, land on the perch and enter the hatchway.

Five pigeons each made several flights, which were filmed and analysed in the same way as in Experiment 1. The field of view of the camera extended about 0.8 m back from the perch and 0.35 m below it. One landing by each bird was chosen for further analysis, in such a way as to give the maximum range of trajectory angles. Each landing yielded between 21 and 25 video fields.

Results

Data from 4 of the upwards landing flights, selected to illustrate the range of patterns obtained, are shown in Fig. 4. The first question to consider is whether head-bobbing occurs during these flights or not. In all cases, a stochastic rhythm in head velocity with a period of 120 ms (±10 ms) is apparent, although there is more high frequency noise superimposed on this rhythm than is seen in level landing flights (Fig. 2; Davies and Green 1988). The power spectra of the head velocity series in all 5 flights (Fig. 5) correspondingly show peak power in the 6–9 Hz region. The results of tests for white noise applied to these series are shown in the second column of Table 1; as in level flights, all but one of the records show a significant periodicity. The exception is the second record in Fig. 4, which is clearly the noisiest.

As in level flights, the rhythm in head velocity cannot be attributed to an oscillation in body velocity with the same frequency and phase. However, body velocity, and particularly its vertical component, show large, irregular changes in some records which are not seen in level landing flights. These are clearest in the first two records in Fig. 4, and are also illustrated in the corresponding power spectra in Fig. 5, which show more power at high frequencies than in level flights. It is not surprising that body velocity should decrease more smoothly during level or slightly downwards landing flights than during flights against gravity, as large accelerations arising during the wingbeat cycle in the latter case will have a greater effect on the vertical component of body velocity.

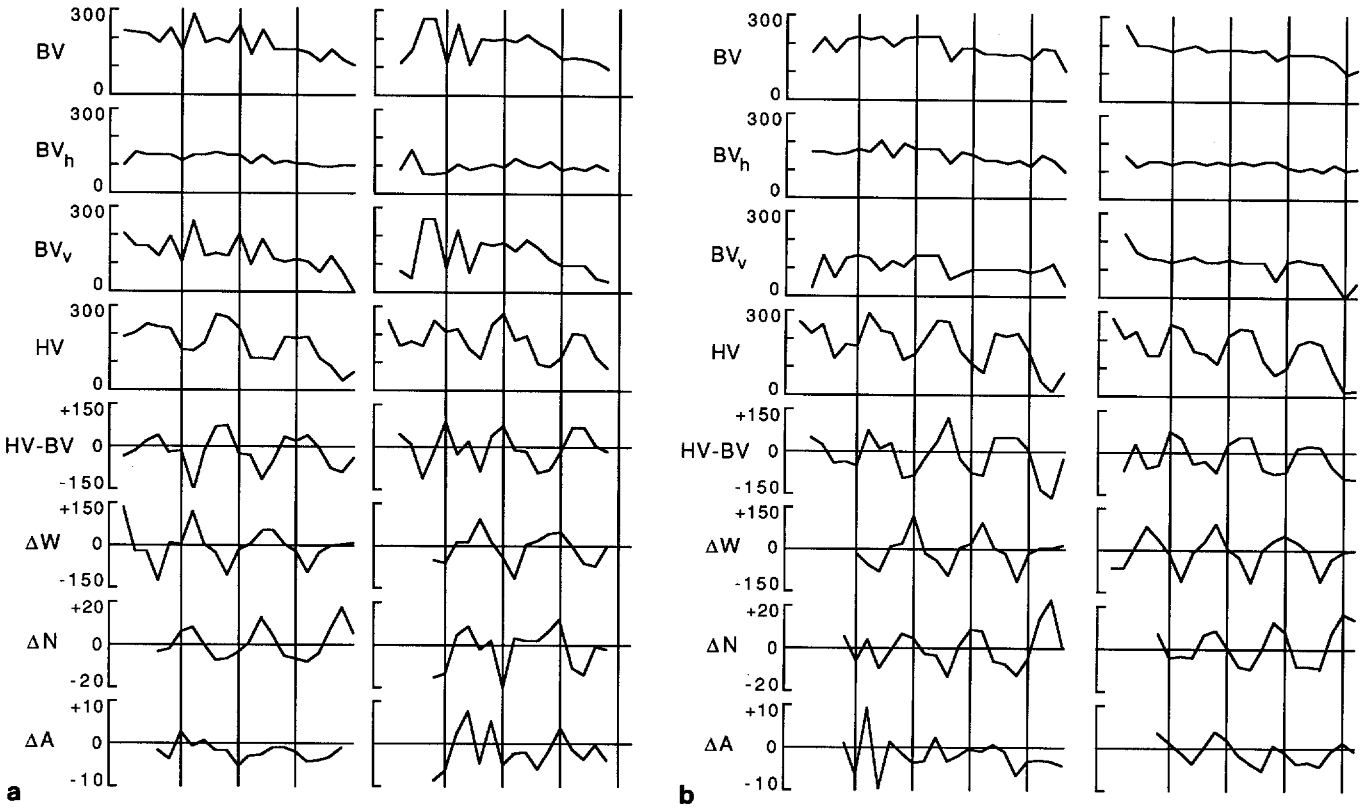

Fig. 4a,b. Data from two upwards landing flights. Labels as in Fig. 2

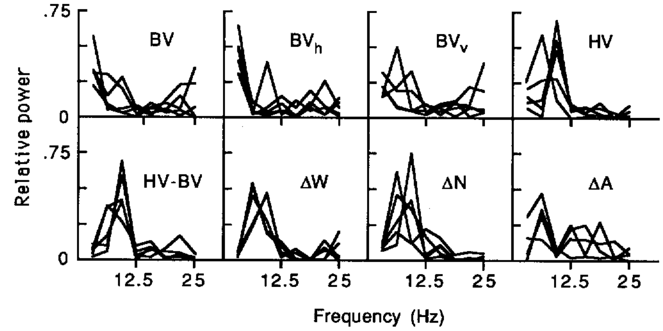

Fig. 5. Frequency domain representation of data from last 340 ms of all 5 upwards landing flights. Labels as in Fig. 2

Turning to the relationship between the head-bobbing and wingbeat cycles, it is clear from Figs. 4 and 5 that, as in level flights, the two occur at the same frequency. However, Fig. 4 suggests that the phase relationship between the two cycles is different from that in level flights. In the upwards flights, the thrust phase of the head-bobbing cycle occurs as the wings move backwards across the midline, between 45° and 90° later in the wingbeat cycle than in level flights.

As in level flights, the attack angle and neck angle data indicate that the head-bobbing rhythm is driven by flexion and extension of the neck, and not by rotation of the body. The four records in Fig. 4 show a consistent relationship between neck angle and head velocity closely similar to that in Fig. 2; the thrust phase of each head-bobbing cycle coincides with a decrease in neck angle as the head is extended forwards relative to the body. Again, no consistent relationship between attack angle and head velocity is apparent. This pattern can also be seen in Fig. 5, where the spectra of the neck angle series all show peak power in the 6–9 Hz region, but those of the attack angle series are less consistent.

Experiment 3

Materials and methods

Upwards flights of a further 12 birds were recorded in the same way as in Experiment 2, but were analysed differently. Individual video frames, 40 ms apart, were photographed from a monitor screen, and a SAC Graf/Bar digitizer was used to obtain from each photograph the X and Y co-ordinates of (i) the centre of the perch, (ii) the centre of the pupil of the eye and (iii) the tip of the beak. Between 9 and 13 frames were obtained from each landing flight.

The co-ordinates obtained from the digitizer were then used to calculate the following parameters (accuracies of measurements are given in brackets): (i) The 'eye-perch distance', between the centre of the pupil and the centre of the perch (± 0.25 cm). (ii) The 'head angle', between the horizontal and the line joining the centre of the pupil and the beak tip ($\pm 3.2°$). (iii) The 'perch angle', between the pupil-beak tip line and the line joining the centre of the pupil to the centre of the perch, positive when the perch lies above the beak tip in the visual field ($\pm 0.7°$). The angular measurements are illustrated in Fig. 6. In frames where the wing obscured the eye, beak tip or both, values were interpolated from adjoining frames.

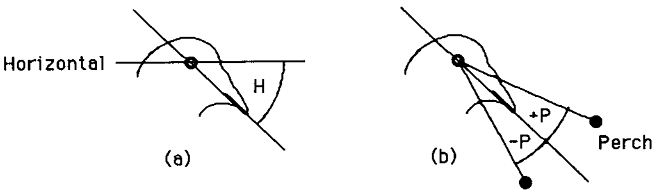

Fig. 6. a Head angle H - the angle between the horizontal and the line joining the centre of the pupil to the beak tip. **b** Perch angle *P* - the angle between the lines joining the centre of the pupil to the beak tip and to the centre of the perch. P is positive when the perch lies above the beak tip and negative when it lies below

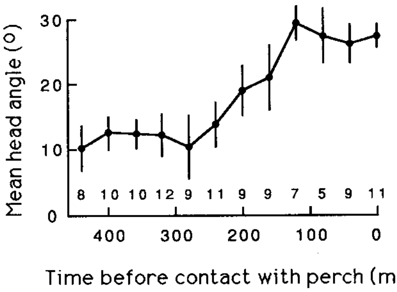

Fig. 7. Mean head angle at 40 ms intervals during upwards flight. *Vertical lines* show standard errors of means. *Numbers below points* are sample sizes

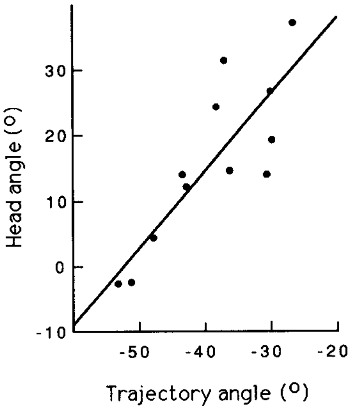

Fig. 8. Relationship between trajectory angle relative to horizontal (negative for upwards flight) and head angle 40 cm from the perch. The *line* is the regression of head angle on trajectory angle

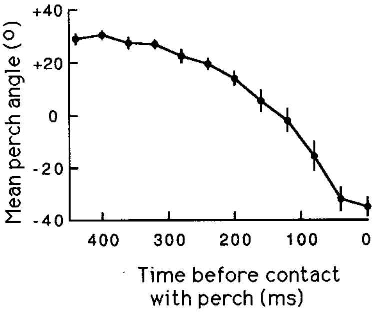

Fig. 9. Mean perch angle at 40 ms intervals before contact with the perch (positive values denote perch above beak tip). *Vertical lines* show standard errors. Sample sizes at each interval are as in Fig. 7

Results

Mean head angle values, at 40 ms intervals up to the first frame in which the feet were in contact with the perch, are shown in Fig. 7. Sample sizes differed between intervals because the wing obscured the eye and beak in some frames, and because video records differed in length, according to the speed of individual birds' approaches. The data show that the head is held at 10–12° to the horizontal at the start of the landing flights and that head angle increases to reach a value just under 30° at contact with the perch. These results contrast with the 35° angle observed during level flight or perching (Erichsen et al. 1989), and the angles greater than 35° observed during downwards landing flights (Green et al. 1992).

In all flights, the trajectory of the eye approximated closely to a straight line, and the lowest value of r obtained from regression of the y co-ordinate of the eye on the x coordinate was 0.995. The angle of this trajectory relative to the horizontal was calculated for each flight as the arctangent of the slope of the reduced major axis of the set of eye coordinates. In both calculations, the coordinates of all visible eye positions, up to and including that at contact with the perch, were used. For consistency with the earlier calculations of trajectory angle for downwards flights (Green et al. 1992), upwards trajectories were assigned *negative* angles, and the value of head angle was taken at the point where the eye was 40 cm from the perch.

Figure 8 shows the relationship between trajectory angle and head angle. There is a significant correlation between the two variables ($r = 0.835$, $df = 10$; $P < 0.001$), and the regression equation for head angle (H) on trajectory angle (T) is $H = 1.18T + 62.0$. As in downwards landing flights, there appears to be a linear relationship between trajectory and head angle. In downwards flights, the effect of rotation of the head is to keep the perch 20–25° above the beak tip in the visual field until about 300 ms before contact (Green et al. 1992). Figure 9 shows the change in mean perch angle (defined in Fig. 6b) for upwards landing flights; until 300 ms before landing, the perch lies between 25° and 30° above the beak tip.

Discussion

Head-bobbing

The results of Experiments 1 and 2 extend earlier work on head-bobbing in landing flight in several ways. They confirm that the 7–8 Hz rhythm in head velocity does not arise from a rhythm in body velocity, or in its horizontal and vertical components. In some upwards flights, fast changes in body velocity occur, mainly in the vertical component, but there is no evidence of a rhythm with the same period as that in head velocity. In level flights, there is a low amplitude rhythm in body velocity, in antiphase to the head-bobbing rhythm, and one possible interpretation of this finding is that the head-bobbing arises from an oscillating rotation of the body in the sagittal plane. Since there is no consistent indication in either upwards or level flights of a 7–8 Hz rhythm in the angle of attack, in phase with head velocity, this possibility can be rejected. However, the 'neck angle' measure does show such a rhythm in all the flights recorded, and has a consistent phase relationship with head velocity. Extension of the neck always coincides with thrust phases of the head-bobbing cycle and flexion of the neck with slow phases.

The main cause of the rhythm in head velocity during both level and upwards landing flights is clearly an oscillating flexion and extension of the neck. Experiments 1 and 2 also demonstrate that this oscillation occurs at the same frequency as the wingbeat cycle and in a consistent phase relationship with it. In level flights, maximum extension of the neck occurs at a mean of 25 ms before the wingtips reach their furthest forward position. There is a suggestion in the results that in upwards flights neck motion is delayed relative to the wingbeat cycle, as the maximum extension of the neck occurs at a mean of 5 ms before the wings are fully forward. The sampling interval makes it difficult to assess the reliability of this difference, and further analysis with finer temporal resolution would be needed to establish whether it is real.

How does the phase-locking of neck flexion/extension and the wingbeat cycle come about? No head-bobbing rhythm occurs during take-off flights from the ground by startled pigeons (Davies and Green 1988); since the only difference between that procedure and the one used here is whether the upwards flight was directed towards a perch or not, it is clear that head-bobbing in flight is associated specifically with approach to a landing target and is not a mechanical or reflex consequence of wingbeat. Instead, there must be some flexible link between the two motor systems. This could come about through the neuronal oscillator driving the wing muscles being coupled and uncoupled to the muscles of the head-neck system. Other possibilities also exist; for example, head-bobbing could be initiated by a tonic muscle contraction or relaxation which allows the mechanical forces caused by wingbeat to set up a passive oscillation in the head-neck system. Testing between these alternatives will clearly require anatomical and physiological methods.

The results of Experiment 2 also contribute to the problem of identifying the function of head-bobbing. The demonstration that head-bobbing occurs in flight specifically when a landing target is approached suggests strongly that the behaviour has a visual function. Since head-bobbing during flight does not stabilize the retinal image, it is likely that it has the function of amplifying optic flow during the thrust phase of each cycle and so increasing the accuracy with which spatial information can be obtained from image motion, as proposed by Frost (1978) and Davies and Green (1988). For example, amplification of motion parallax may enable a pigeon to detect more accurately small-scale features of a perch such as its fine texture, which could be significant in providing information about its load-bearing properties.

Another possibility is that head-bobbing may provide a means of controlling visually a pigeon's approach to a perch. Lee et al. (1993) show that the accelerations of the images of a bird's feet and of a perch over the retina, generated by the head-bobbing cycle, are a potential source of information about the trajectory of the feet relative to the perch. In particular, if these accelerations are equal, then the feet are following a trajectory passing through the perch. If they are not, the relationship between the signs of the two accelerations specifies whether the trajectory of the feet passes over or under the perch, and therefore what correction to flight is required. Whether head-bobbing in landing flight has either or both of these specific functions is a problem for further research, but it is clear that the behaviour contributes in some way to the visual control of landing.

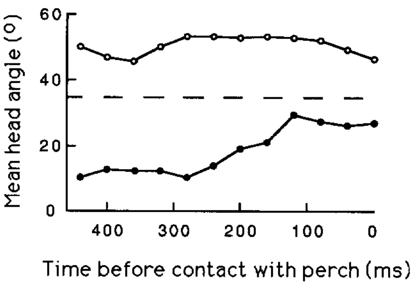

Fig. 10. Mean head angle at 40 ms intervals before contact with the perch in upwards (●) and downwards (○) flights (data from Fig. 7 and Green et al. 1992, respectively). *Broken line* - head angle (35°) in level flight or perching

Head orientation

The results of Experiment 3 show that a linear relationship between flight trajectory and head orientation is maintained over a wider range of trajectories than previously shown (Green et al. 1992). In particular, the head is turned upwards from its normal position and towards the horizontal during upwards landing flight. The contrast between head orientation in upwards and in downwards flights is seen in Fig. 10, which compares the present results and those of Green et al. (1992). The effect of head orientation on the position of the perch in the visual field is similar to that in downwards flights; until about 300 ms before contact, the perch lies 25–30° above the beak tip, about 5° more than in downwards flights.

These findings are consistent with Green et al.'s conclusion that the change in head orientation with trajectory does not bring the image of the perch onto any specialized retinal area. When the perch is between 25° and 30° above the beak tip and roughly in the median plane, its image falls neither in the area centralis nor in the area dorsalis, or red field (Hayes et al. 1987). The results are also consistent with the possibility that head orientation serves to maximize binocular information about the perch, by keeping it close to the elevation (20°) where there is the greatest binocular overlap in pigeons of the strain used here (Martin and Young 1983). Even so, the width of the binocular field decreases only gradually on either side of this peak, so that the change in head orientation from 35° would make little difference to the length of the perch falling in both monocular visual fields.

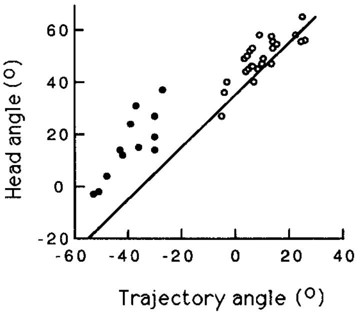

Fig. 11. Relationship between trajectory angle and head angle 40 cm from the perch for upwards (●) and downwards (○) flights (data from Fig. 8 and Green et al. 1992, respectively). *Diagonal line* - relationship predicted ($H = T + 35$) if head orientation keeps the perch in focus

In the case of downwards flights, Green et al. (1992) proposed that a more promising explanation for the relationship between head orientation and trajectory is that it serves to keep the perch in focus as the bird approaches it, without the need for accommodation. The data which they obtained for head and trajectory angles lie close to the line $H = T + 35$, the predicted relationship if the perch is kept in focus (see Fig. 11). Interestingly, however, the present results are not consistent with this hypothesis. In upwards flights, the head angles observed are between 10° and 30° greater than predicted (see Fig. 11). In other words, the head is not turned far enough upwards to bring the perch far enough down in the visual field for it to lie at the far point of the eye. This can be confirmed by comparing the measured distance between eye and perch with the far point calculated at the elevation of the perch from Fitzke et al.'s (1985) equation. In downwards flights, these do not differ by more than 2 cm during the last 200 ms of landing flight (Green et al. 1992), whereas in the upwards flights recorded in Experiment 3 the difference is 24 cm at the start of this period and falls to 1.3 cm at contact.

While it is possible that head orientation in downwards flights has the function of keeping the perch in focus during approach, this explanation cannot be generalized to upwards flights, where the perch lies beyond the far point of the unaccommodated eye until the feet contact it. None of the hypotheses considered so far therefore provides a satisfactory single explanation for the observed relationship between trajectory and head angle. One further possibility which should be considered in future work is that head orientation and head-bobbing during landing flight have a *common* function. If the function of head-bobbing is to maximize optic flow during the thrust phase, then the axis along which the head travels relative to the body during the thrust phase must be kept parallel to the bird's flight trajectory. Any discrepancy will result in a lower vector sum of body velocity and head velocity relative to the body, and therefore less amplification of optic flow.

This argument implies that a bird is faced with the problem of extending its neck in such a way that its head travels along a straight axis parallel to its flight trajectory, and of maintaining this performance over a wide range of trajectories. Rotation of the head relative to the body may be necessary in order to achieve this, given the constraints imposed by the functional anatomy of the neck (Elshoud and Zweers 1987; Zweers et al. 1987). Further investigation of this hypothesis would require a detailed analysis of the kinematics of the head-neck system during head-bobbing, of the kind already achieved for behaviour patterns such as pecking and drinking (Heidweiller et al. 1992).

Acknowledgements. We are grateful to Mike Burton, Howard Martin, Claire O'Malley and Andy Smith for help with programming frame-grabbing and digitizing equipment, to Teresa Sharp and Sarah Orchard for their expert care of the pigeons, and to Jake Kennedy and Steve Tristram for photographic assistance. We also thank an anonymous referee for valuable suggestions for further analyses of the data.

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