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Head Orientation in Pigeons During Landing Flight

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Landing flights of pigeons were video recorded or filmed, and frame-by-frame measurements were made of the angle of the head relative to the horizontal, and of the position of the perch in the visual field. The angle of the head increases above that seen in free flight, to a value which is correlated with the trajectory of approach to the perch. As a result, the perch is fixated 20–25° above the beak early in landing flight. The possible significance of the behaviour is discussed in relation to specialised retinal areas and to lower-field myopia.

Pigeon Landing flight Head orientation Binocular visual field Lower field myopia Visuomotor control

Erichsen, Hodos, Evinger, Bessette and Phillips (1989) recently investigated the head postures of pigeons (*Columba livia*) during a number of activities, and found that the head is held at a similar angle to the horizontal during flight, walking, perching and standing. The angle between the horizontal and a line passing from the centre of the pupil to the bill tip was, on average, 35° across the four conditions. Hodos and Erichsen (1990) provide an explanation for this constant head angle, drawing on the finding of Fitzke, Hayes, Hodos and Holden (1985) that there is a gradient of myopia in the pigeon's visual field. With the eye–bill tip line 35° below the horizontal, the eye is emmetropic for objects on or above the horizon, but increasingly myopic at angles below the horizontal. Fitzke *et al.*'s measurements of the refractive state of the eye fitted the curve given by:

$$R = \sin A / h \tag{1}$$

where R is the myopia (in D), A is the angle below the horizontal and $h = 0.194$ m. Fitzke *et al.* (1985) showed that this value of h corresponds closely to the mean height of pigeons' eyes above the ground in their normal standing posture. Therefore, points on a level ground surface at any distance from a pigeon will be in focus, without any accommodation of the eye, since the distance of a point on the ground is given by $h/\sin A$. Fitzke *et al.* (1985) suggest that the constant head posture adopted by walking and standing pigeons serves to keep the ground surface and horizon in focus, while the same posture in flight keeps the horizon in focus but not the ground.

Most of Erichsen *et al.*'s (1989) records of head posture in flight were made during level flight, but in a few cases birds began to land while being filmed. In these cases, the head angle was greater, averaging 50° below the horizontal. Our aim was to follow up this finding by measuring moment-to-moment changes in head posture during landing flight and their effect on the position of the perch in the visual field.

METHODS

Sixteen birds were used, 5 drawn from one colony of homing pigeons (*Columba livia*) and 11 from another. The birds were of both sexes, varying in age from 1 yr 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 birds used were familiar with the apparatus and with the procedure of being filmed while making landing flights. The rear wall of the cage, parallel to the flight path, was covered with a white screen with horizontal calibration lines.

Each bird made one landing flight, and was filmed in natural daylight using a Panasonic MV7 solid state video camera, with an electronic shutter providing an exposure time of 1 msec. In the first five flights, the field of view of the camera included the last 50 cm of approach, while for the remainder the last 90 cm of approach was recorded. Each landing yielded between 7 and 15 video frames, 40 msec apart, depending upon field of view and approach speed. Individual fields from the first five flights were printed in colour as hard copies using a Sony video printer, while those from the remaining flights were photographed from a monitor screen. A SAC Graf/Bar digitiser was then used to obtain from each

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print or photograph the X and Y co-ordinates of (i) the centre of the perch, (ii) the centre of the pupil of the eye, (iii) the tip of the beak, (iv) the crissum (base of the tail), and (v) the tip of the leading toe.

The co-ordinates obtained from the digitiser were then used to calculate the following parameters: (i) The distance between the centre of the pupil and the centre of the perch ("eye-perch distance"). (ii) The angle between the horizontal and the line joining the centre of the pupil and the beak tip ["head angle" shown in Fig. 1(a)]. (iii) The angle between the pupil–beak tip line and the line joining the centre of the pupil to the centre of the perch ("perch angle"). The perch angle is positive when the perch lies above the beak tip in the visual field [see Fig. 1(b)].

Data were also obtained from a sample of 12 cine film records made in earlier research on the timing of foot extension during landing flight (Davies & Green, 1990). The pigeons filmed were drawn from the same colony as the first five birds recorded on video, but were not individually identified, so that the number of different birds filmed is not known. The cine films were made in the same way as the video records, but using 16 mm Kodak Tri-X reversal film in a Beaulieu R16 automatic camera, running at 52.5 frames sec^{-1}. Angles and distances were then measured directly from the screen of a Vanguard film analyser. These film records provided slightly poorer image quality, resulting from the longer exposure time of each frame (approx. 8 msec). The centre of the pupil could be located accurately in each frame, but the tip of the beak was slightly blurred and so measurement error is greater than in the video records.

RESULTS AND DISCUSSION

Head angle during landing flight

In each flight, the first video frame in which the feet were in contact with the perch was identified, and values of head angles were measured at 40 msec (one frame) intervals before this point. Figure 2 shows mean head

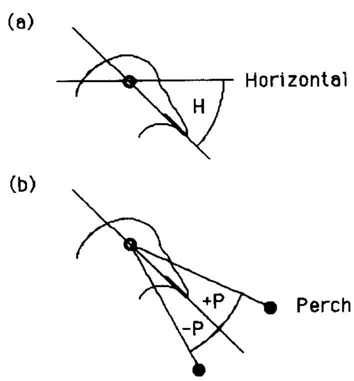

FIGURE 1. (a) Head angle H is defined as the angle between the horizontal and the line joining the centre of the pupil to the beak tip. (b) Perch angle P is defined as the angle between the lines joining the centre of the pupil to the beak tip and to the centre of the perch. P is positive when the perch lies above the beak tip and negative when it lies below.

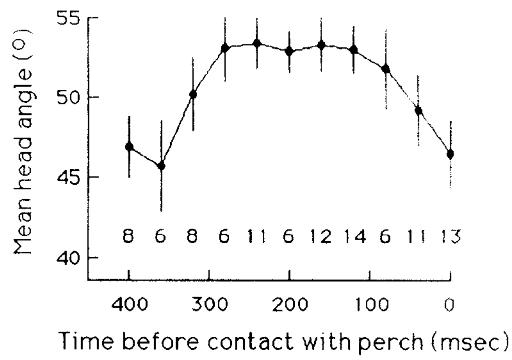

FIGURE 2. Mean head angle at 40 msec intervals before contact with the perch. Vertical lines show SEMs. Numbers below points are sample sizes.

angles for all flights at 40 msec intervals before contact with the perch. Sample size varies from one interval to another for two reasons. First, video records differed in length, according to the field of view and the speed of individual birds' approaches. Second, the wing is raised above eye level and obscures the head once during each wingbeat cycle (Davies & Green, 1988; Erichsen *et al.*, 1989). Typically, eye and beak were obscured by the wing in one out of every three consecutive images.

The data confirm Erichsen *et al.*'s (1989) report that the head is held at a greater angle relative to the horizontal during landing flight than during level flight. Between 280 and 80 msec before landing, mean head angle lies between 50 and 53°, some 15–18° more than the angle characteristic of level flight. The possibility that this population of birds have an unusually large head angle in all situations can be discounted for two reasons. First, the data show an increase in head angle as the perch is approached, and a decrease towards the angle characteristic of perching pigeons (Erichsen *et al.*, 1989) just before landing.

Second, the data show a specific relationship between the head angle attained on a flight and the trajectory of approach. This can be demonstrated by calculating the angle between the horizontal and the path followed by a bird's eye on a particular landing. For each landing, linear regressions were carried out of the y co-ordinate of the eye on the x co-ordinate, using all available frames up to and including contact with the perch. In all cases, the successive eye positions approximated closely to a straight line; mean r was 0.971 and the lowest single r value was 0.928. The gradient of the regression line was then used to compute for each flight the angle between the line and the horizontal. This "trajectory angle" was assigned a positive value for a downwards flight.

The relationship between trajectory and head posture was examined by taking a single value of head angle from the later part of each flight. Values were chosen in two ways: (i) the value of head angle 120 msec before contact with the perch, interpolating from adjacent values where the raised wing obscured the head in this frame; (ii) the value of head angle when the eye was at 40 cm from the perch, determined by linear interpolation from adjacent frames. As well as data from the 16 video recorded flights, 12 data points were also included from

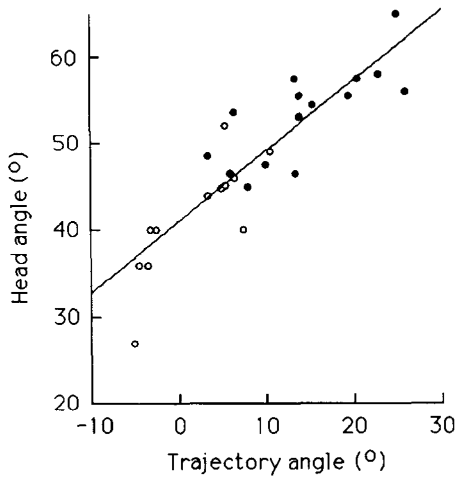

FIGURE 3. Relationship between trajectory angle (positive for a downwards flight) and head angle 40 cm from the perch. Solid circles, data from 16 video recorded flights by different birds; open circles, data from 12 filmed flights by an unknown number of different birds. The regression of head angle on trajectory angle is shown.

earlier film records. These were obtained using a different method of encouraging the pigeons to fly, which resulted in lower trajectory angles than in the later experiment, and so they provide a wider overall range of trajectory angles.

Correlation coefficients were then calculated between each of these head angles and trajectory angle, and a strong correlation was found in both cases (for head angle at 40 cm from the perch, $r = 0.871$, d.f. $= 14$, $P < 0.001$; for head angle at 120 msec before contact, $r = 0.845$, d.f. $= 14$, $P < 0.001$). Note that the significance of the correlation coefficients are tested using 14 deg of freedom; this is because individual birds were not identified in the film records, and it is not known how many different birds are included in the sample. We have therefore made the most conservative possible assumption that of the total of 28 flights, only 16 different birds are involved. Figure 3 shows the relationship between trajectory angle and head angle at 40 cm from the perch. The regression of head angle on trajectory angle yields the equation $H = 0.821T + 41.0$.

Position of the perch in the visual field

Head angle increases during landing flight, and the angle reached at 40 cm or 120 msec before landing is positively correlated with the angle of the bird's trajectory. A possible function of this behaviour is to fixate the image of the perch on some particular part of the retina. Figure 4(a) shows how perch angle (the angular position of the perch in the visual field relative to the beak tip) changes during landing flight. Until 280 msec before landing, the perch lies between 20 and 25° above the beak tip. After this point, perch angle falls smoothly to about 35° below the beak on landing.

The geometrical relationship between perch angle and a bird's position relative to the perch can be seen directly in Fig. 4(b), which gives values of perch angle calculated at eye–perch distances 10 cm apart. These were obtained by linear interpolation between adjacent perch angle measurements. The overall pattern is similar to that of Fig. 4(a), and indicates that the perch falls between 20 and 25° above the beak until a pigeon's eye is 50 cm from the perch. Figure 4(b) also provides a comparison with the perch angle values which would be expected if the birds had followed the same flight path but had maintained a head angle of 35° throughout. As head angle measurements from these birds in free flight were not available, the published average of 35° (Erichsen *et al.*, 1989) was used. It is clear from Fig. 4(b) that the increased head angle in landing flight raises the perch substantially in the visual field, to the region 20–25° above the beak when the bird is in the range 80–60 cm from the perch.

Head angle and lower field myopia

The increase in head angle observed during landing may have the function of bringing the perch into a region of the visual field 20–25° above the beak, but there is one feature of the data which suggests that a *further* function may be involved. If pigeons adopt a head angle which fixates the perch in this region for as long as possible, then we would expect to see all birds increase their head angle to some maximum value, at which it was no longer possible, for either anatomical or aerodynamic

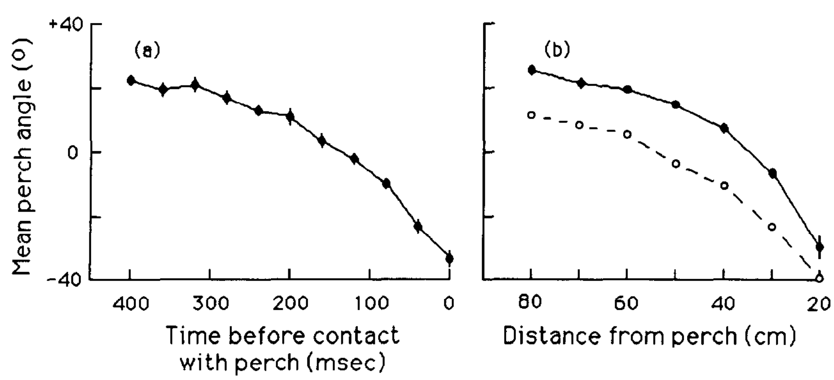

FIGURE 4. (a) Mean perch angle at 40 msec intervals before contact with the perch (positive values denote perch above beak tip). (b) Solid circles, mean perch angle at 10 cm intervals before contact with the perch; open circles, mean values for perch angle calculated for birds following same flight path but maintaining a head angle of 35°. In both sets of data, vertical lines show standard errors and sample sizes at each interval are as shown in Fig. 2.

reasons, to increase it any further. When this maximum head angle was reached, fixation of the perch above the beak would then be lost. This would occur sooner in a steep flight than in a shallow one, but head angle should reach the same maximum value whatever the trajectory. This does not happen; the *maximum* head angle reached during each flight is correlated just as strongly as the measures of head angle used earlier ($r = 0.747$, d.f. = 14, $P < 0.001$).

Is there another possible reason why head angle during landing should be closely related to trajectory angle? One reason is suggested by the evidence for a gradient of myopia in the pigeon's lower visual field, following equation (1) above (Fitzke *et al.*, 1985). Consider first a pigeon flying horizontally with a head angle of 35° and an unaccommodated eye [Fig. 5(a)]. There will be a horizontal plane 19.4 cm below the bird's eye, on which any object will be in focus. Note that this plane is horizontal only if the head angle is 35°; it will tilt with the head if its angle changes. If a pigeon approaches a perch in such a way that its eye follows a straight horizontal path, then the perch will remain in focus if this path passes 19.4 cm above it.

Consider next the geometry of a downwards approach to a perch [Fig. 5(b)]. What conditions are necessary now to maintain the perch in focus? The plane on which points are in focus must be tilted so as to lie parallel to the path traced by the eye during approach flight, and this can be achieved simply by turning the head downwards from the "level flight" angle of 35° by the trajectory angle T between eye path and horizontal. Conversely, for an upwards approach to a perch, the head must be turned upwards, reducing its angle to the horizontal by T.

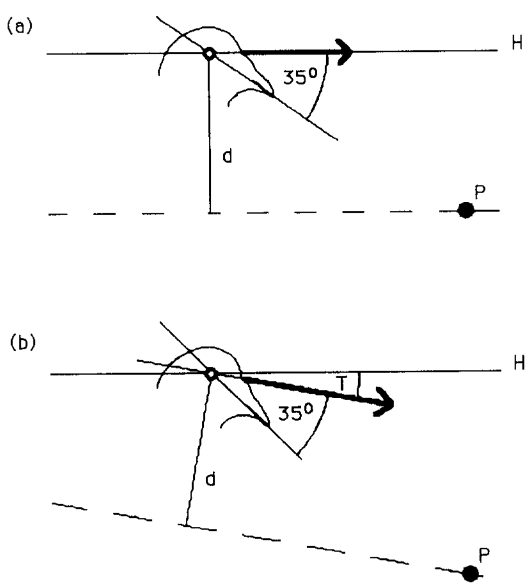

FIGURE 5. Schematic representations of pigeon flying towards perch (P) along path indicated by heavy arrow. (a) Horizontal flight. With a head angle of 35°, all points on the horizontal plane denoted by the broken line will be in focus. (b) Downwards flight, along path inclined at angle T to the horizon. With a head angle of $35 + T$°, all points on the plane denoted by the broken line, parallel to the path of travel, will be in focus.

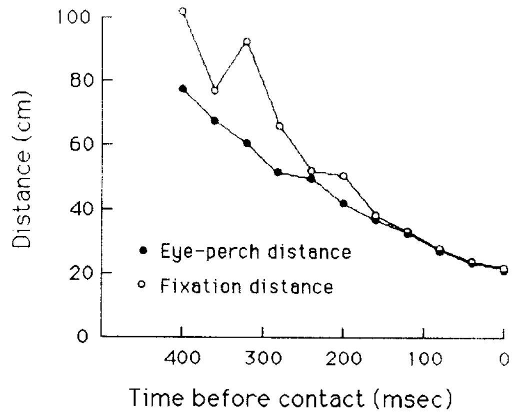

FIGURE 6. Measured values of eye–perch distance and calculated values of fixation distance, assuming resting accommodation, at 40 msec intervals before contact with the perch.

This argument suggests that the function of the greater head angle in downwards landing flights may be to ensure that the perch remains in focus during the approach. This hypothesis makes a specific prediction about the relationship between head angle H and trajectory angle T; the two angles should be positively correlated and should be related by the equation:

$$H = T + 35^\circ. \qquad (2)$$

This equation corresponds closely to the regression line obtained from the data shown in Fig. 3, suggesting that the head is rotated to an angle which keeps the perch in focus as the bird lands. This hypothesis can be tested more directly by comparing the distance of the perch from the eye with the "fixation distance" at which the eye is focussed, assuming resting accommodation. The fixation distance FD can be calculated (in m), for the average bird, by applying Fitzke *et al.*'s (1985) findings:

$$FD = 0.194/\sin(35 - P) \qquad (3)$$

where P is the perch angle as defined above.

The measured values of eye-perch distance and the calculated values of fixation distance are shown in Fig. 6; the two curves coincide closely, showing that the perch is maintained in focus, without the need for accommodation, throughout the last 160 msec of landing flight. The match between fixation distance and eye–perch distance was close in individual flights as well as in the mean data. Over the last 160 msec, the mean absolute (modulus) difference between the two values was 2.8 cm.

It is possible to make an estimate of the depth of field for each value of fixation distance; the range of distances over which blurring of an object may be undetectable to a pigeon. The perch falls within this range at 360 and 240 msec before contact, and from 160 msec onwards. It should be emphasised that these estimates of depth of field cannot be relied upon heavily. They are based upon Green, Powers and Banks' (1980) calculation of 0.3 D for the depth of focus of the pigeon eye, based on published values for focal length, pupil aperture and minimum resolvable blur circle on the retina. The last of these must be estimated from the psychophysically determined acuity of the pigeon, which may vary from task to task and be effectively lower in this context than in other acuity tasks. Campbell (1957), for example, obtained a value of 0.3 D for human depth of focus, compared to a value of about 0.1 D predicted from acuity measurements. If pigeons' ability to detect blur is also less than that predicted from psychophysical measurements, the implication is that the perch is in focus for a larger part of landing flight than indicated above.

GENERAL DISCUSSION

We consider four possible functions for pigeons' head posture during landing flight. First, do pigeons adopt a head posture which fixates the perch in the same retinal area as a pecking target is fixated? Just before a peck, a target is fixated within a few degrees of the beak tip (Goodale, 1983; Erichsen *et al.*, 1989), and this region of visual space projects onto the temporal retina, just outside the area dorsalis, or "red field" (Hayes, Hodos, Holden & Low, 1987). Hayes *et al.* suggest that images of pecking targets on the ground fall in the red field just before the target is fixated, which accords with the hypothesis (e.g. Friedman, 1975; Nye, 1973) that this retinal area provides acute near vision, while the area centralis is used for distance vision.

The results obtained here do not fit into this proposed scheme. Until a pigeon is within 50 cm of a perch, its image falls on the retina some distance below the red field. At an elevation of 20–25° above the beak, the image would fall near the area centralis only if the perch were at an azimuth of 60–70° from the frontal meridian. Although we could not measure azimuth accurately, it was clear from the photographs that it did not vary by more than a few degrees from the frontal meridian. We conclude that distance vision, in the context of landing flight, does not require fixation of the perch in either the red field or the area centralis.

Second, could the retinal elevation of the perch during landing be significant for binocular vision? Martin and Young (1983) found the greatest extent of overlap of the visual fields of the two eyes of pigeons to be 27°, at 20° above the beak tip. Although these results conflict with those of Martinoya, Rey and Block (1981), who found the greatest binocular overlap below the beak tip, Martin and Young (1983) conclude that differences between pigeon strains are the most likely explanation for the discrepancy. The birds used here were, like Martin and Young's, English Racing Homers.

The hypothesis that the perch is fixated at 20–25° above the beak tip in order to take advantage of binocular overlap is consistent with evidence that binocular disparity is a possible cue timing landing flight in pigeons (Davies & Green, 1990, 1991). However, a difficulty for the hypothesis is the fact that the width of the binocular field falls only gradually at elevations above or below 20°. Martin and Young's (1983) data show that, for a pigeon 80 cm from the perch used in this experiment, fixation of the perch at 20° above the beak tip would result in 40 cm of its width falling in the binocular field, a figure only 3 cm greater than if the head were kept in the level flight posture. This small extra overlap is unlikely to make any difference to a pigeon's ability to judge the distance of the segment of the perch on which it will land.

Third, the argument that increased head angle during landing flight keeps the perch in focus without the need for accommodation is supported by the data in Fig. 6. These show a remarkably close correspondence between perch distance and calculated fixation distance throughout the last 240 msec of landing, but, even so, there is a difficulty with this interpretation. The formula used to calculate fixation distances is that giving the best fit to Fitzke *et al.*'s (1985) data for the relationship between retinal elevation and myopia, but those data show some scatter of individual measurements of refractive state at each retinal elevation. The range of values of myopia at elevations corresponding to the perch angles we measured 100–200 msec before landing is about 2 D. If the refractive states of the eyes of the birds used here vary to the same extent, then the fixation distances during this part of landing flight will vary over a range of about 25–50 cm.

Such variation in refractive state would imply that many birds did not keep the perch in focus unless the eyes accommodated. Only those birds with refractive characteristics close to the average would keep the perch in focus solely by increasing head angle. Further, it is possible that Fitzke *et al.*'s (1985) measurements may underestimate the variability of lower field myopia in pigeons (Schaeffel, 1992). If so, the argument that increased head angle keeps the perch in focus is further weakened. This question cannot be resolved with the present data alone, and would require comparison of individual birds' refractive states with their head postures during landing.

Finally, a fourth possibility is that the increased head angle during landing does not have a purely visual function, such as maximising binocular overlap or keeping the perch in focus, but instead contributes to the visuomotor co-ordination involved in attaining a stable perching posture. A consequence of the match between eye–perch distance and calculated fixation distance is that, in the last 240 msec of landing, the image of the perch sweeps over the retina along the same path as would the image of a point on the ground at the same distance when approached by a walking bird. The degree of focus of the image may vary between birds, but the relation between retinal position and the position of the bird's eye relative to the perch will vary very little.

It may be, therefore, that increased head angle plays some role in a visuomotor mechanism which brings the bird's head into the same geometric relations to the perch as would obtain if it were walking on a plane passing through it. Such a mechanism might simplify the motor control problem of co-ordinating the leg, flight and tail muscles to bring the bird's body into a stable perching posture, by recruiting mechanisms of motor co-ordination used in the maintenance of a stable standing posture.

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