J. exp. Biol. **180**, 85-104 (1993)
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VISUAL CONTROL OF VELOCITY OF APPROACH BY PIGEONS WHEN LANDING

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Accepted 5 March 1993

Summary

Films of pigeons flying to a perch were analysed to test a theory of how speed of approach and timing of foot extension in preparation for landing are visually controlled. Rapid neural computation of distance to perch and of speed and deceleration would seem to be required. However, according to the theory, none of this is necessary. Simpler control is possible based solely on the value of the tau function of certain optic variables x, where the tau function of x is x divided by its rate of change; i.e. $\tau(x)=x/\dot{x}$. $\tau(x)$ is a first-order approximation of time to contact with the perch and so could be used for timing foot extension. Controlled braking is possible by simply keeping $\dot{\tau}(x)$, the rate of change of $\tau(x)$, constant. The results indicated that pigeons did regulate their braking when approaching the perch by keeping $\dot{\tau}(x)$ constant and initiated foot extension when $\tau(x)$ reached a threshold value of approximately 150ms. They followed this procedure even when they had one eye covered, and so binocular vision was not necessary for regulating braking or timing foot extension. It is shown that an optic variable that the pigeons could be using is the width of the optic projection of the gap between foot and perch. It is further shown that they could be using the same optic variable for controlling the trajectory of their feet to contact the perch.

Introduction

In order to land successfully, a bird must regulate visually its speed and direction of approach to a perch, and time appropriately manoeuvres such as the extension of its feet. Davies and Green (1990) analysed the visual control of foot extension in pigeons and hawks, using a method devised by Wagner (1982). By taking measurements from films of houseflies approaching a landing target, Wagner calculated in each frame the values of several optical parameters, including the distance, retinal velocity and rate of retinal dilation of the target. This last parameter is equivalent to τ, which provides a first-order approximation of time-to-contact (Lee, 1980). Wagner argued that the optical parameter controlling landing would show less variation than the others just before the initiation of landing, and his results showed that τ varied less than other parameters at this stage. This

Key words: pigeon, visuomotor behaviour, flight control, approach, *Columba livia*.

finding indicates that flies may extract the value of τ from visual input and use the value of τ to trigger landing. Borst and Bahde (1988) have proposed and presented evidence for an alternative model for the triggering of landing behaviour in flies, based on the spatio-temporal integration of movement detectors' output signals. However, their results are not strictly comparable with Wagner's, since the flies were tethered while small discs were moved towards them but did not contact them, whereas in Wagner's experiments the flies were free-flying and physically landing on a surface.

In Davies and Green's (1990) analysis of birds' landing flights, τ varied less than either distance or angular velocity just before landing in hawks, but distance varied least in pigeons. Davies and Green argued that the rhythmic oscillation of the head relative to the body (head-bobbing) observed in pigeon landing flight (Davies and Green, 1988) caused greater variation in head velocity in pigeons than in hawks, which were shown not to head-bob. The implication was that head-bobbing may prevent the use of τ as a means of timing landing accurately, although in further experiments Davies and Green (1991) found that pigeons switch to the use of τ when landing with monocular vision or when stressed by tape being placed near the eyes.

Whereas previous work on the visual control of birds' landing manoeuvres has concentrated on the timing of a single discrete action – the extension of the feet – the present analysis is concerned primarily with a different aspect of landing, the control of braking. Braking appropriately is important: if the bird brakes too hard it will stop short, drop and miss the perch; if it does not brake hard enough it will be unable to check its momentum when its feet hit the perch and will tip forward. In either case injury could result. We will first outline a theory of how the bird might visually control its braking and then present evidence testing the theory from film analyses of pigeons landing.

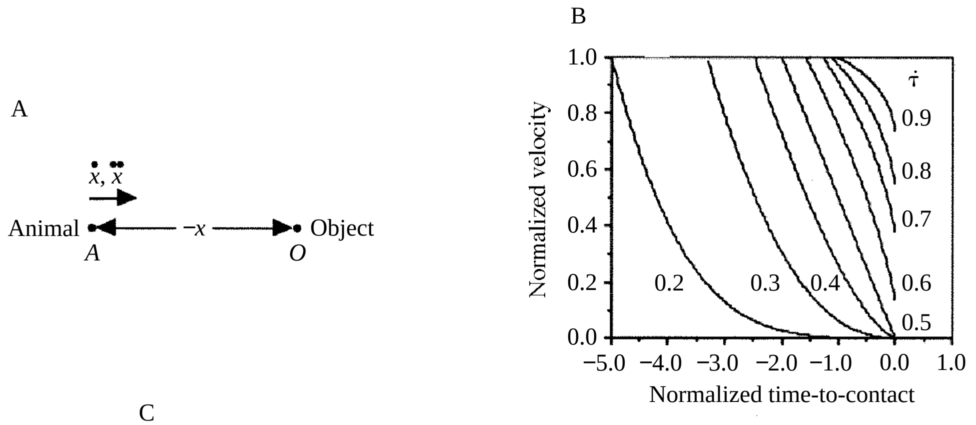
Theory of control of speed of approach

Controlling speed of approach to a destination, as when a bird lands on a perch or a driver stops behind another vehicle, is intrinsic to many locomotor acts. To illustrate the theory of control of speed of approach, we will consider the linear approach of an animal to a surface. The theory, however, applies to approach along any dimension, including curvilinear approach and rotary approach along the angular dimension, as when an animal turns to orientate. The implications of the theory are summarized in Fig. 1 and details are given in Appendix 1.

Constant deceleration approach

We start by considering what might appear the simplest way of controlling approach, by maintaining constant deceleration. Referring to Fig. 1A, suppose at a certain time an animal A is at a distance $-x$ from a destination O and is approaching O at speed $\dot{x}$. Suppose it now starts decelerating at constant deceleration $-\ddot{x}$ (>0). Then its stopping distance will be $-\dot{x}^2/(2\ddot{x})$ and so it will stop short of, stop at, or collide with O according to whether $-\dot{x}^2/(2\ddot{x})$ is less than, equal to, or greater than $-x$. Therefore, to stop at O, for instance, it would appear to have to know its distance away ($-x$) and its speed of approach ($\dot{x}$) to set its deceleration ($-\ddot{x}$) appropriately.

However, this is not necessary. A simpler solution exists.



C

Value of $\dot{\tau}$	Implied movement of animal	Effect of keeping acceleration/ deceleration constant	Effect of keeping $\dot{\tau}$ constant
$\dot{\tau}>1$	Accelerating	Collides ($\dot{\tau}$ decreases to 1)	Collides
$\dot{\tau}=1$	Constant velocity	Collides ($\dot{\tau}$ constant)	Collides
$0.5<\dot{\tau}<1$	Decelerating	Collides ($\dot{\tau}$ increases to 1)	Controlled collision (braking increases)
$\dot{\tau}=0.5$	Decelerating	Stops at	Stops at (braking constant)
$0<\dot{\tau}<0.5$	Decelerating	Stops short ($\dot{\tau}$ decreases)	Stops at (braking decreases)

Fig. 1. (A) Notation for linear approach. At time *t*, the animal has coordinate x (<0) and is approaching destination with velocity $\dot{x}$ (>0) and acceleration $\ddot{x}$ ($\dot{x} = dx/dt$, $\ddot{x} = d^2x/dt^2$). Tau function of $x=\tau(x)=x/\dot{x}$. Rate of change of $\tau(x)=\dot{\tau}(x)$. (B) Curves showing how normalized velocity would change over time if approach were controlled by keeping $\dot{\tau}(x)$ constant at the different values shown (see Appendix 1 for equations of curves). (C) Summary of implications of the theory of control of speed of approach described in text.

The tau function

The ratio of the animal's distance away from O ($-x$) to its speed of approach ($\dot{x}$) provides a first-order estimate of its time-to-contact with *O*. If the speed of approach were to stay constant, then the ratio provides an accurate estimate, but if speed decreases or increases the ratio respectively under- or over-estimates time-to-contact. The ratio has been termed the *tau-margin* (Lee and Young, 1986). For the more general theory, we here use the idea of the *tau function* of x, defined as x divided by its rate of change over time ($\dot{x}$). In symbols:

$$\tau(x) = x/\dot{x} \tag{1}$$

It has been shown that, in theory, the value of $\tau(x)$ is directly derivable from the optic flow field and does not need to be computed from information about distance and speed (see Lee, 1976; Tresilian, 1990). Likewise, visual perceptual experiments using simulations of approaching surfaces have shown that the value of $\tau(x)$ can be perceived from the display without information about distance or speed of the approaching surface (Schiff and Detwiler, 1979; Todd, 1981). Experiments indicate that optically specified $\tau(x)$ is used to time interception of moving objects by humans (Bootsma and van Wieringen, 1990; Lacquaniti and Maiolo, 1989; Lee *et al.* 1983; Savelsbergh *et al.* 1991) and to time locomotor actions when approaching surfaces by birds (Lee and Reddish, 1981) and humans (Lee *et al.* 1982; Sidaway *et al.* 1989; Warren *et al.* 1986).

Stopping at a destination

The rate of change with respect to time of $\tau(x)$ [$=\dot{\tau}(x)$] is a dimensionless quantity with the interesting property of providing information for controlling braking (see Appendix 1 for details). To avoid collision, all that is in principle necessary is to register the value of $\dot{\tau}(x)$, adjust braking so that $\dot{\tau}(x) \leqslant 0.5$ and then keep braking (and hence deceleration) constant. This procedure would generally result in stopping short of the surface (see Fig. 1C).

A general procedure to *stop at* a surface is again to adjust braking so that $\dot{\tau}(x) \leqslant 0.5$ but now to keep $\dot{\tau}(x)$ – and not braking – constant (Fig. 1B,C). This procedure requires the brakes to be steadily slackened off as the surface is approached (except for $k=0.5$, when deceleration is constant). Analysis of braking behaviour of test drivers indicated that they followed the stop-at procedure with $\dot{\tau}(x)=0.425$ (Lee, 1976).

Controlling collision

If $\dot{\tau}(x)$ is kept constant at a value of k between 0.5 and 1.0, then braking has to get progressively *harder* as the destination is approached. In fact, stopping at a destination in this way theoretically requires reaching infinite braking force. A realistic procedure – the *controlled-collision procedure* – is to keep $\dot{\tau}(x)$ constant at a value between 0.5 and 1.0 until maximum braking power is reached, and then to maintain this braking force. This would result in the animal colliding with the destination but in a controlled way (Fig. 1B,C).

Film analysis of a hummingbird aerial-docking on a feeder tube indicated that it followed the controlled-collision procedure; as it braked it held $\dot{\tau}(x)$ constant at a mean value of 0.71 and its bill passed into the feeder rather than stopping at the opening (Lee *et al.* 1991). It has also been shown (Kim *et al.* 1992) that a person can judge from a computer simulation of approach to a surface with $\dot{\tau}(x)$ held constant at different values (but with no information about distance, speed and deceleration of approach) whether the approach would result in a 'soft collision' [$\dot{\tau}(x) \leqslant 0.5$] or a 'hard collision' [$\dot{\tau}(x) > 0.5$].

Aims of the experiments

From measurements of pigeons' approach to a perch, we set out to determine whether they maintain a constant braking force or whether they adjust braking force in such a way as to hold $\dot{\tau}(x)$ constant. In the first case, a plot of $\dot{x}$ against time should be linear and that of $\dot{\tau}(x)$ against time should be non-linear [except when $\dot{\tau}(x)=0.5$; see Fig. 1C]. In the second case, the plot of $\tau(x)$ against time should be linear and the plot of $\dot{x}$ against time should be generally non-linear [again, except when $\dot{\tau}(x)=0.5$]. We carried out this analysis on landing flights made with normal vision and with one eye covered in order to determine to what extent binocular vision is required for controlling approach.

We also sought to determine whether extension of the feet as the bird comes in to land is activated at a particular value of $\tau(x)$, of distance ($-x$) or of time to contact t_c with the perch. [Note that, at each instant when the bird is decelerating approaching the perch, $\tau(x)$ will be shorter than the time to contact t_c, since $\tau(x)$ equals the time to contact if the approach velocity were to remain constant.] Davies and Green (1990) measured $\tau(x)$ and distance using successive positions of the eye, and the results suggested that, when pigeons land with normal vision, distance is the effective parameter. Here, our aim was to determine whether the same is true if the variables are measured using a point on the body which is not affected by head-bobbing.

Materials and methods

Measurements were taken from the films of pigeons landing used in Davies and Green's (1990, 1991) analyses. The films were taken at 52.5 frames s^{-1} while birds flew a distance of 3.3 m through a flight cage towards a cylindrical perch 75 cm long and 2 cm in diameter. As well as making normal landing flights, each bird was also filmed landing with temporary monocular vision, in order to test for any effect of removing binocular information specifying perch distance. In a third condition, intended to control for the possibility that any effect of monocular occlusion was of a non-specific kind, birds landed with a cover placed near an eye but not obscuring frontal vision.

After making normal landings, birds flew several times in the control occlusion (CO) condition, with thin strips of masking tape placed around the eye so as to form a rough circle. The tape was pressed flat against the feathers and below the level of the orbital skin so as to prevent occlusion of the visual field, particularly the frontal field. Birds then flew under monocular occlusion (MO), with one eye completely covered by masking tape, and protected by a layer of Sterispon no. 1 absorbable gelatin sponge between eye and tape. At the end of each flight, the tape was checked by presenting a fast looming object to the occluded eye; the absence of any reaction was taken as evidence that the eye cover was intact. In conditions CO and MO, flights were divided roughly equally according to whether the left or the right eye was occluded.

The overall landing performance of the birds in conditions CO and MO was not obviously different from that observed in normal landings. In both cases, accuracy in landing on the perch did not appear to be affected, and the head-bobbing movements seen in landing flight (Davies and Green, 1988) occurred normally. Fifteen records of normal flight, 16 from condition CO and 15 from condition MO proved suitable for further analysis.

In previous work, films were analysed by recording in each frame the coordinates of the centre of the bird's eye relative to the centre of the perch. Measurements of speed, acceleration and τ obtained in this way would be affected by head-bobbing, and so it was necessary to take a reference point on the body which would be minimally influenced by the head-bobbing rhythm. The point chosen, termed the breast point, was the furthest forward protrusion of the sternum.

Calculating $\dot{x}$ and $\tau(x)$ during approach to the perch

Fig. 2A–E shows a sequence of film frames of a pigeon approaching the perch in the present experiment. The frames run from 247ms before the feet contacted the perch to 19ms before contact. The interframe interval is 57ms. It can be seen that during the flight the head changes its position relative to the breast: the head is forward in Fig. 2A, back in Fig. 2B and so on. This is because the head was bobbing (at about 8Hz) as the pigeon came in to land (Davies and Green, 1988). The feet also move relative to the breast. Notably, in Fig. 2C, which corresponds to 133ms before contact, the feet start to extend forward preparatory to landing.

Film measurements of the movement of points on the head, breast and foot showed that each point oscillated slightly forward and back as the bird moved towards the perch. The amplitude of oscillation of the breast point was only about 5mm, compared with an amplitude of about 25mm for the head and about 12mm for the feet. Thus, movement of the breast point gives a good measure of the movement of the bird as a whole towards the perch.

Fig. 2F shows some typical approach paths of the breast point. The paths were in general quite straight but were inclined downward at various angles between 1° and 24° to the horizontal. In calculating $\dot{x}$ and $\tau(x)$, first the approach path was approximated by the straight line regression of the Y-coordinate of the breast point on the X-coordinate. The regression line invariably passed above the perch. x was defined as the distance of the breast point to the plane passing through the perch and perpendicular to this linear approximation to the approach path. Thus, x was the distance of the breast point to its (linearly approximated) point of nearest approach to the perch. For each separate approach, x, $\dot{x}$ and $\tau(x)$ were calculated at each sample point from the (X,Y) coordinates of the breast point relative to the centre of the perch, as follows.

(1) The X and Y time series were smoothed using a Butterworth filter (Wood, 1982) with 6Hz cut-off to give time series X_s, Y_s. (The filter tended to eliminate the approximately 8Hz oscillation of the breast point which accompanied the head-bobbing, but the amplitude of this oscillation was negligibly small at about 5mm.)

(2) The slope, m, of the linear regression of Y_s on X_s was calculated.

(3) x was calculated as $x=(X_s+mY_s)/\sqrt{(1+m^2)}$.

(4) The time series of x was differentiated to give $\dot{x}$, using the formula: $\dot{x}_n=(x_n-x_{n-1})/(0.019)$.

(5) $\tau(x)$ was first calculated as $\tau(x_{\text{breast}})=x/\dot{x}$. This assumes that the birds were controlling the movement of the breast point to a destination at the closest point of approach the perch (i.e. where x=0).

(6) $\tau(x)$ was also calculated as $\tau(x_{\text{feet,lp}})=(x_{\text{breast}}-x_{\text{breast at contact}})/\dot{x}_{\text{breast}}$, where $x_{\text{breast at contact}}$ is the coordinate of breast point in the frame in which the feet first contacted the perch. This assumes that the birds were controlling the movement of the landing position of the feet – coordinate $x_{\text{feet,lp}}$ – to a destination at the perch (where $x_{\text{feet,lp}}=0$).

Results

Testing the constant $\dot{\tau}(x)$ *hypothesis*

The hypothesis that braking is controlled by keeping $\dot{\tau}(x)$ constant predicts that during deceleration $\tau(x)$ will approach zero linearly with time to contact. The constant deceleration hypothesis, in contrast, predicts that speed ($\dot{x}$) will decrease linearly with time to contact.

Fig. 3 shows the plots of $\tau(x_{\text{breast}})$, $\tau(x_{\text{feet,lp}})$ and $\dot{x}_{\text{breast}}$ against time-to-contact of the feet with the perch for individual flights under the three experimental conditions. Table 1 gives the means and standard deviations of the linear regressions of the plots. Under each experimental condition three results were obtained.

(1) The values of r^2 for both the $\tau(x_{\text{breast}})$ and the $\tau(x_{\text{feet,lp}})$ regressions were close to unity, the value corresponding to perfect linearity. However, the values of r^2 were significantly higher for the $\tau(x_{\text{feet,lp}})$ regressions ($P<0.005$, paired *t*-test).

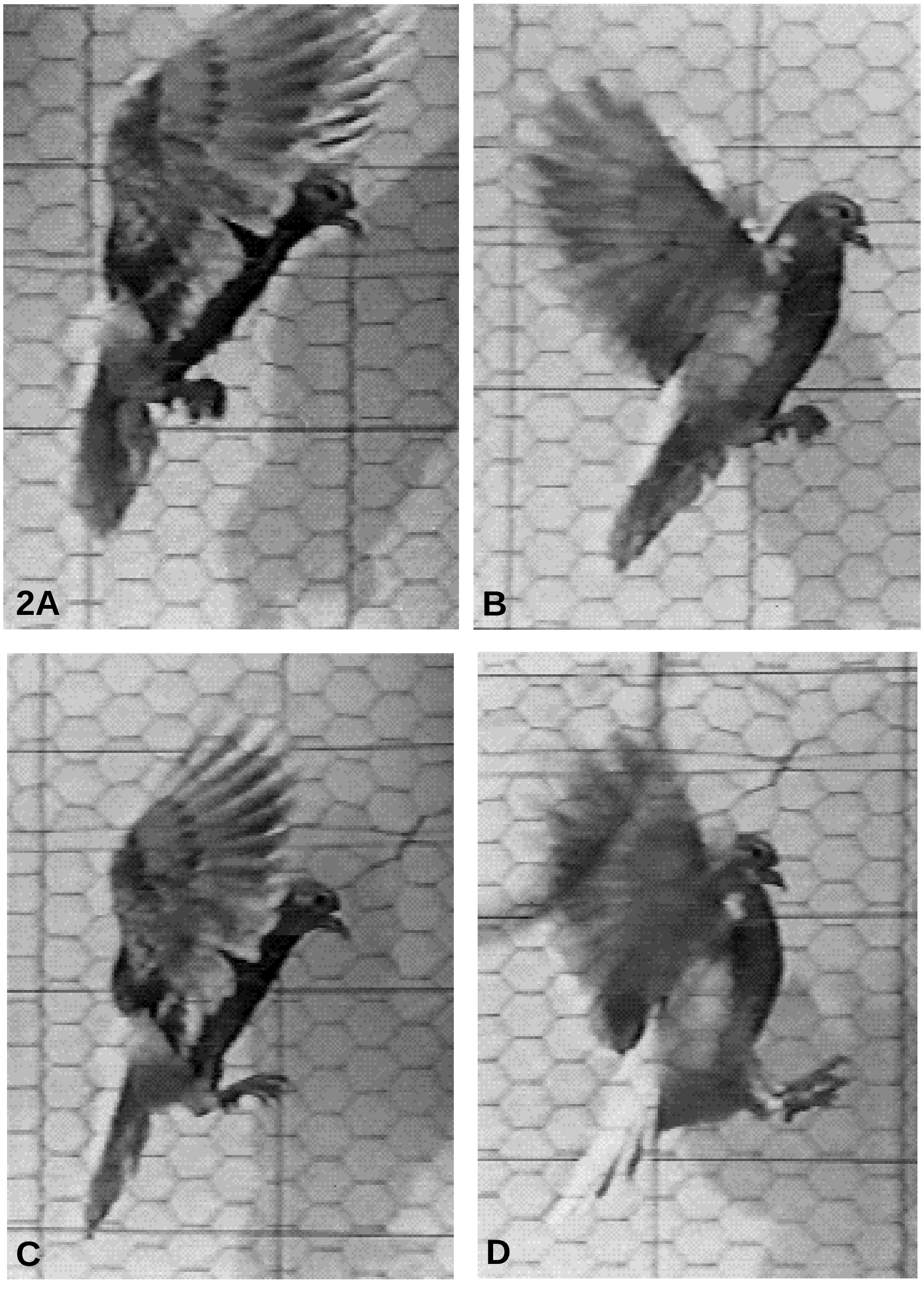
(2) The mean intercepts were not significantly different from zero for the $\tau(x_{\text{feet,lp}})$ regressions but were for the $\tau(x_{\text{breast}})$ regressions ($P<0.001$, *t*-test). Although the difference in the intercepts could have been due to the way $\tau(x_{\text{feet,lp}})$ was calculated (i.e. $x_{\text{feet,lp}}$ was zero at landing), the significantly higher r^2 value for the $\tau(x_{\text{feet,lp}})$ regressions cannot be so explained.

(3) The values of r^2 for both the $\tau(x_{\text{feet,lp}})$ and $\tau(x_{\text{breast}})$ regressions were significantly higher than the r^2 values for the corresponding $\dot{x}$ regressions ($P<0.01$ and $P<0.05$, respectively, *t*-test). Also, the plots of $\dot{x}$ against time (Fig. 3) are of the form predicted if $\dot{\tau}(x)$ were being kept constant (Fig. 1C): the slope steepens as the perch is approached, corresponding to braking getting harder.

These three results indicate that the pigeons controlled deceleration by keeping $\tau(x_{\text{feet,lp}})$ constant, as against keeping deceleration ($\ddot{x}$) or $\dot{\tau}(x_{\text{breast}})$ constant. The fact that the regression slopes (Table 1), which are estimates of the constant $\dot{\tau}(x_{\text{feet,lp}})$ values, were significantly greater than 0.5 and less than 1.0 in all conditions ($P<0.001$, *t*-test) indicates that the birds were flying on a controlled collision course with the perch. This agrees with the velocity graphs in Fig. 3, which show that the birds were moving forward slowly as their feet contacted the perch.

Timing of foot extension

In previous analyses of these flights, Davies and Green (1990, 1991) obtained evidence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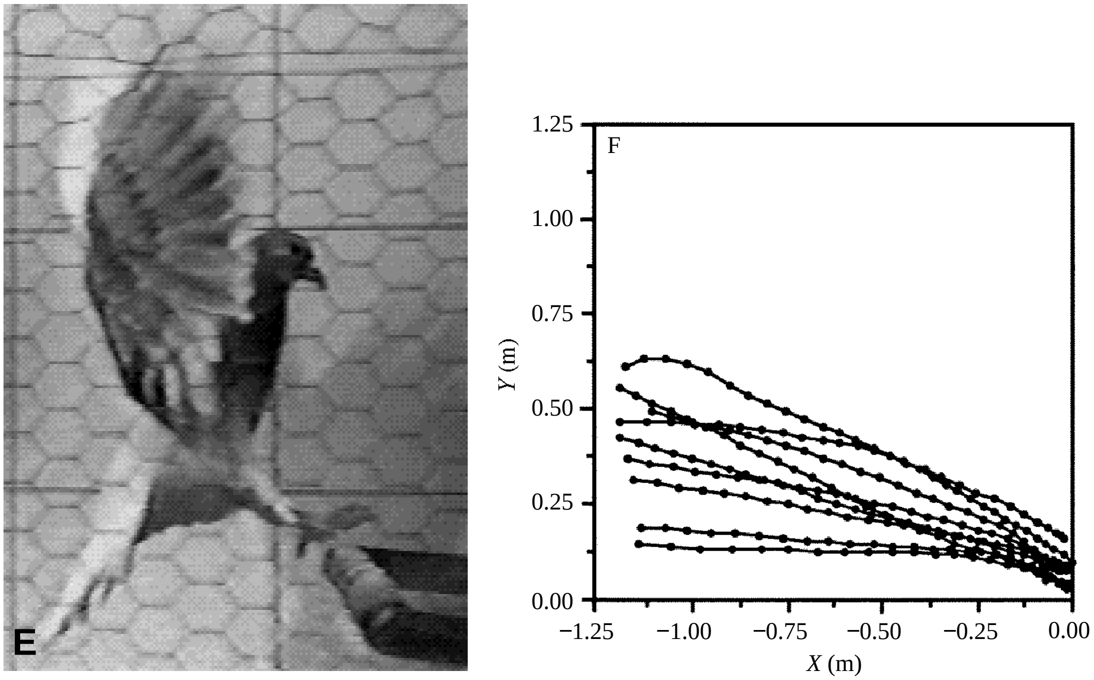

Fig. 2. (A–E) Sequence of film frames of a pigeon approaching the perch in the present experiment. The first frame is at 247ms before the feet contacted the perch, the last frame is at 19ms to contact, and the inter-frame interval is 57ms. Foot extension started at C, 133ms to contact. (F) Typical trajectories of the point on the breast during normal approach to the perch [coordinates (0,0)]. Time interval between the marked data points is 19ms. The duration of the trajectories shown is about 500ms.

Table 1. *Means (standard deviations) of coefficients of linear regressions of* $\tau(x_{breast})$*,* $\tau(x_{feet,lp})$ *and velocity* $\dot{x}_{breast}$ *on time-to-contact of feet with perch under the three experimental conditions*

		$\tau(x_{\mathrm{breast}})$	$\tau(x_{\mathrm{feet,lp}})$	$\dot{x}_{\mathrm{breast}}$
Normal	r^2	0.982 (0.017)	0.992 (0.011)	0.893 (0.124)
(N=15)	Slope	0.719 (0.094)	0.775 (0.109)	0.220 (0.091) ($\mathrm{m\,s^{-2}}$)
	Intercept	−0.033 (0.022) (s)	0.006 (0.029) (s)	−0.057 (0.012) ($\mathrm{m\,s^{-1}}$)
Monocular	r^2	0.971 (0.042)	0.987 (0.031)	0.841 (0.130)
control	Slope	0.770 (0.098)	0.814 (0.082)	0.135 (0.055) ($\mathrm{m\,s^{-2}}$)
(N=16)	Intercept	−0.045 (0.030) (s)	−0.001 (0.009) (s)	−0.048 (0.007) ($\mathrm{m\,s^{-1}}$)
Monocular	r^2	0.945 (0.054)	0.980 (0.035)	0.869 (0.125)
(N=15)	Slope	0.722 (0.169)	0.792 (0.144)	0.122 (0.056) ($\mathrm{m\,s^{-2}}$)
	Intercept	−0.071 (0.044) (s)	−0.003 (0.019) (s)	−0.040 (0.012) ($\mathrm{m\,s^{-1}}$)

Regressions are for data shown in Fig. 3.
Units of coefficients given in parentheses; if not so indicated, coefficient is dimensionless.

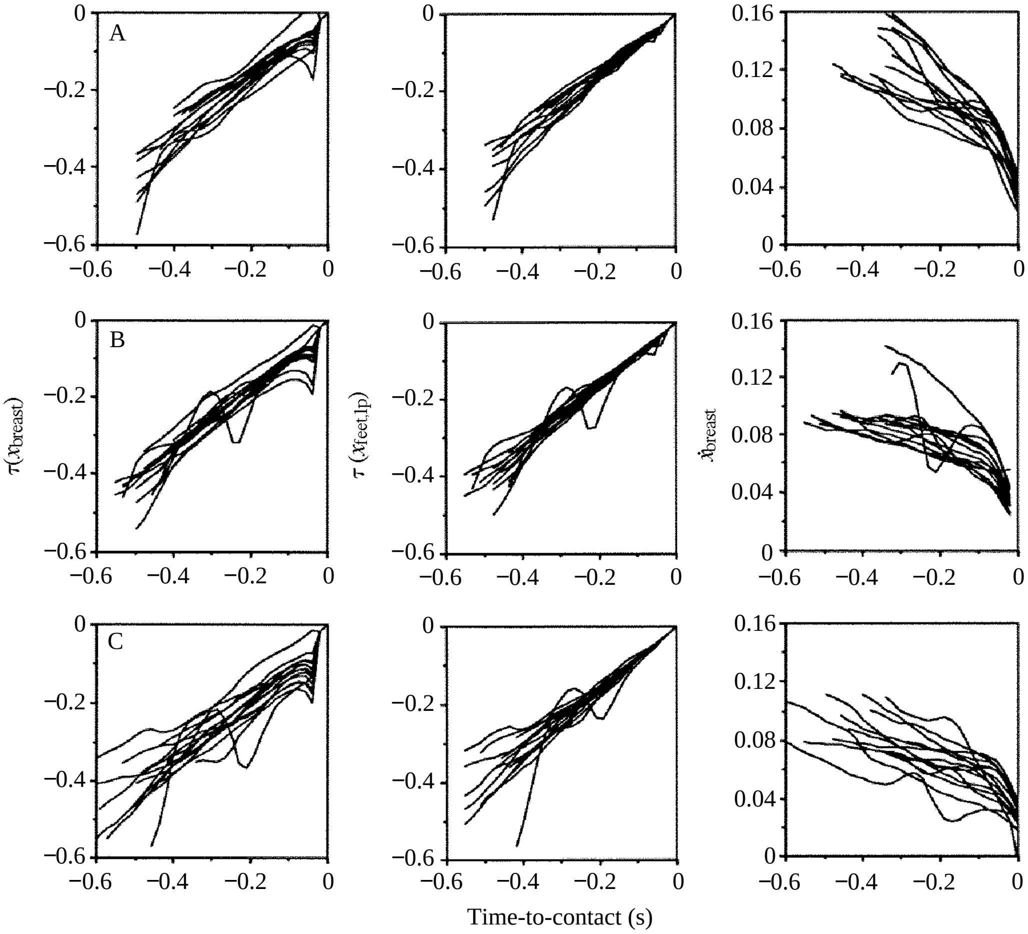

Fig. 3. Plots of $\tau(x_{\text{breast}})$, $\tau(x_{\text{feet,lp}})$ and $\dot{x}_{\text{breast}}$ against time-to-contact of the feet with the perch for all the individual flights under the three experimental conditions: A, normal vision; B, control occlusion; C, monocular occlusion. In general, the $\tau(x_{\text{feet,lp}})$ plots were highly linear, the $\tau(x_{\text{breast}})$ plots were a little less so and the $\dot{x}_{\text{breast}}$ plots were even less linear (regression coefficients given in Table 1). The data thus support the hypothesis that the birds were adjusting braking force to hold $\dot{\tau}(x_{\text{feet,lp}})$ constant, as against keeping $\dot{\tau}(x_{\text{breast}})$ or deceleration $(-\ddot{x})$ constant.

that foot extension was governed by the distance between eye and perch in normal conditions, but by τ of that distance [i.e. $\tau(x_{\text{eye}})$] in the two occlusion conditions. The finding that braking during landing flight is controlled so as to hold $\dot{\tau}(x_{\text{feet,lp}})$ constant suggested that it would be interesting to look again at foot extension and compare variation of distance and variation of $\tau(x_{\text{feet,lp}})$ rather than $\tau(x_{\text{eye}})$.

Foot extension was identified as the interval between frames in which the greatest increase occurred in the distance between the crissum (base of the tail) and the toes. The index of dispersion (standard deviation/mean) was calculated for $x_{\text{feet,lp}}$, $\tau(x_{\text{feet,lp}})$ and time to contact with the perch at foot extension and in each of the preceding frames.

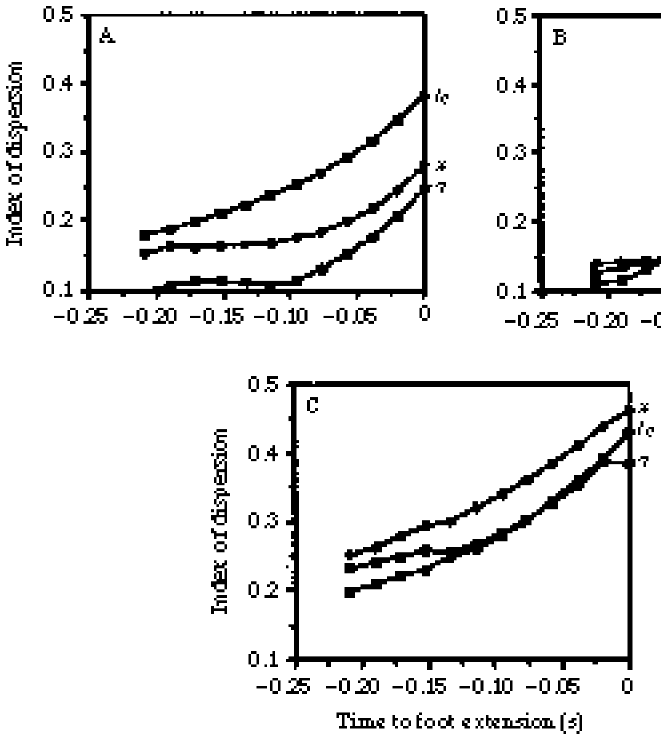

Fig. 4. Index of dispersion (standard deviation/mean) for $x_{\mathrm{feet,lp}}$, $\tau(x_{\mathrm{feet,lp}})$ and time to contact (t_c) with the perch at foot extension (time 0 on abscissa) and at preceding times, under the three experimental conditions: A, normal vision; B, control occlusion; C, monocular occlusion. Under normal vision, index of dispersion was consistently lowest for $\tau(x_{\mathrm{feet,lp}})$, indicating that foot extension is governed by $\tau(x_{\mathrm{feet,lp}})$ as against distance from perch ($x_{\mathrm{feet,lp}}$) or time to contact with perch (t_c).

Fig. 4 shows the results for flights in the three conditions. In normal flight, $\tau(x_{\mathrm{feet,lp}})$ has the lowest index of dispersion of the three variables, indicating that the feet were extended when $\tau(x_{\mathrm{feet,lp}})$ reached a threshold value. The mean value of $\tau(x_{\mathrm{feet,lp}})$ when the feet were extended was 87ms (S.D. 21ms). If we take 60ms as an estimate of visuomotor delay (Davies and Green, 1990), the threshold value was approximately 150ms.

Thus, in normal flight, the pattern of results obtained here is the opposite of that obtained by Davies and Green (1990), where the index of dispersion for $\tau(x_{\mathrm{eye}})$ was greater than that for distance. The difference arises from the different ways of measuring the parameters in the two cases, using eye position in the earlier work to give x_{eye} and $\tau(x_{\mathrm{eye}})$, but landing position of the feet here to give $x_{\mathrm{feet,lp}}$ and $\tau(x_{\mathrm{feet,lp}})$. It is not surprising that $\tau(x_{\mathrm{eye}})$ yields higher indices of dispersion than $\tau(x_{\mathrm{feet,lp}})$ because the head-bobbing rhythm causes an approximately twofold variation in $\tau(x_{\mathrm{eye}})$ over a single head-bob cycle.

Effect of interfering with vision

To test whether covering one eye significantly affected control of braking, the monocular occlusion (MO) condition was compared against the control occlusion (CO) condition. None of the $\tau(x_{\mathrm{feet,lp}})$ regression coefficients (Table 1) differed significantly (*t*-test) between the conditions. Thus, with one eye covered, $\tau(x_{\mathrm{feet,lp}})$ was still maintained constant during approach. This control of $\tau(x_{\mathrm{feet,lp}})$ was also unaffected by the attachment of tape near the eye: the $\tau(x_{\mathrm{feet,lp}})$ regression coefficients for normal and CO flights were not significantly different (*t*-test; see Table 1).

As regards timing of foot extension, the indices of dispersion of distance $x_{\mathrm{feet,lp}}$, $\tau(x_{\mathrm{feet,lp}})$ and time to contact at different intervals before the feet were extended are shown in Fig. 4. The curves lie closer together in conditions CO and MO than in the case of normal vision, and a likely explanation is that the birds were flying more slowly in conditions CO and MO (Davies and Green, 1991) and with less deceleration (compare right-hand panels of Fig. 3). As a result, variation in speed was lower and so distance and speed were more nearly proportional; this, by itself, would make the indices of dispersion close in value. The mean of $\tau(x_{\mathrm{feet,lp}})$ when the feet were extended was 124ms (S.D. 38ms) in condition CO and 149ms (S.D. 57ms) in condition MO, compared with 87ms (S.D. 21ms) with normal vision. The difference between the means for CO and MO was not significant (*t*-test). However, both means were significantly greater than the mean under normal vision ($P<0.01$, two-tailed *t*-test). To summarize, interfering with vision by covering one eye or by having tape near the eye appeared to make the birds more cautious, in that they approached the perch more slowly, braked more gently and extended their feet sooner before contact.

Although the slower landing approach of the birds in condition MO brings the curves for the indices of dispersion of time to contact and τ closer together, the index of dispersion of distance 60ms before foot extension lies just as far above that of τ as when birds have normal vision. We can conclude that the timing of foot extension by $\tau(x_{\mathrm{feet,lp}})$, like the regulation of braking by $\dot{\tau}(x_{\mathrm{feet,lp}})$, does not require binocular vision.

In condition CO, the index of dispersion for distance is lower than that for τ, 60ms before foot extension. There is no apparent explanation for this result, and the small difference in the two indices, caused by the birds' slow approach speed, suggests that these data may not reflect a real change in visual control of landing flight.

Discussion

The results indicate that the pigeons regulated their braking when approaching the perch by keeping the dimensionless variable $\dot{\tau}(x_{\mathrm{feet,lp}})$ constant and initiated foot extension when $\tau(x_{\mathrm{feet,lp}})$ reached a threshold value (approximately 150ms when they had normal vision). This procedure was followed whether the bird had normal vision or had one eye covered, and so binocular vision was not necessary for regulating braking or timing foot extension.

What optical information is available to pigeons to detect values of $\tau(x_{\mathrm{feet,lp}})$ and $\dot{\tau}(x_{\mathrm{feet,lp}})$? $\tau(x)$ *measured at the eye* is the ratio of eye–perch distance to eye speed, and is equivalent to the tau function of the size of the image of the perch on the retina (Lee, 1980). As discussed earlier, however, this optical parameter fluctuates in value during landing flight as a result of head-bobbing, and there is evidence that it is *not* used to time landing manoeuvres under normal circumstances (Davies and Green, 1990). However, the value of $\tau(x_{\mathrm{feet,lp}})$ is specified optically by a different variable – the tau function of the retinal separation of the images of feet and perch – and this variable is unaffected by head-bobbing. We next demonstrate this relationship and also show that head-bobbing can contribute to the control of a bird's approach to a perch.

Bobbing to land

Head-bobbing appears at first to make the visual guidance of landing more difficult. It occurs at about 8Hz with an amplitude of about 25mm (Davies and Green, 1988), which means that the eyes are subject to accelerations up to about $6\boldsymbol{g}$. Because of the speed of landing flight, head-bobbing does not fix the eyes relative to the environment for a period in each cycle, as it does when pigeons are walking, and so the function of the behaviour cannot be to stabilize the retinal image. Is it possible that head-bobbing actually assists in the visual control of landing flight, whatever visual functions it may have in other contexts? One possibility is that it provides a means of guiding the feet towards the perch, as we will next demonstrate.

Fig. 5 shows a schematic eye of a pigeon. The nodal point of the lens is at *E* and the flat 'retina' is parallel to the instantaneous direction of travel of the bird. A flat retina is chosen simply for mathematical convenience: the argument applies in principle to a retina of any shape (see Appendix 2). Onto the 'retina' are projected images of the feet and of the perch to which the bird is flying. Inspection of films of the birds flying indicated that, during the head-bob cycle, the feet were visible to the bird most of the time, both before and after they had been stretched forward in landing. In Fig. 2A–D the feet are clearly

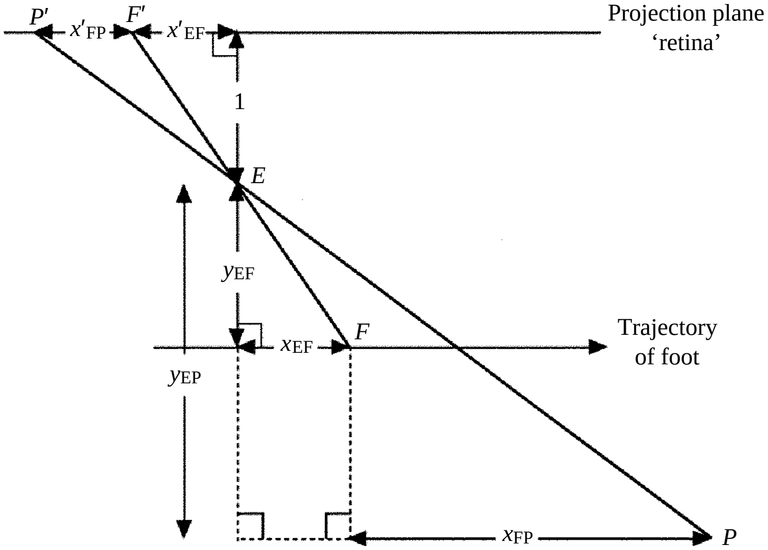

Fig. 5. Optical variables providing information for controlling flight path to a perch and regulating braking. See Discussion and Appendix 2 for details.

visible to the pigeon; in Fig. 2B, where the head is at the back of the bob cycle, the feet are marginally visible to the bird.

In Fig. 5, P is a point on the perch to which the bird is flying. F is the landing position of the feet – the point in the pigeon's body space which the centre of the foot occupies when it is stretched forward in landing. It is assumed that the pigeon has sufficient body sense that it can determine the visual direction of F from the visual direction of the foot even before the foot is stretched forward in landing. The optic projection (real or virtual) of F is F', and the optic projection of P is P'.

In Fig. 5, F is on a course that will pass above perch point P. However, the course might equally well have been drawn so that F passed below P or – which is the pigeon's aim – directly towards P. How are the different types of course optically specified by the events on the 'retina'? A simple answer lies in two optic variables: (1) the acceleration $\ddot{x}'_{\mathrm{EF}}$ of the image of F relative to the centre of the retina and (2) the acceleration $\ddot{x}'_{\mathrm{FP}}$ of the image of F relative to the image of the perch P. A point to note is that the optic acceleration $\ddot{x}'_{\mathrm{EF}}$ is determined solely by the acceleration of the eye relative to the foot. It therefore provides an intrinsic metric against which to measure the other optic acceleration $\ddot{x}'_{\mathrm{FP}}$. The latter reflects the movement of the foot relative to the perch, which is what the bird requires information about.

As shown in Appendix 2, to direct the flight path of the feet towards the perch it is sufficient to regulate flight until the optic acceleration $\ddot{x}'_{\mathrm{FP}}$ of the image of the feet relative to the image of the perch is zero. If at any time $\ddot{x}'_{\mathrm{FP}}$ is not equal to 0, then if $\ddot{x}'_{\mathrm{FP}}$ and $\ddot{x}'_{\mathrm{EF}}$ are both accelerations or both decelerations the flight path needs to be lowered, otherwise the flight path needs to be raised. Notice that this theory does not require accurate measurement of optical accelerations. All that is required is to determine whether accelerations are zero, negative or positive.

If head-bobbing contributes to the control of landing trajectory by generating optical accelerations, how are the problems of controlling braking and of timing foot extension solved? The theory developed here provides a straightforward answer. The optic distance x'_{FP} between the images of the landing position F of the foot and of perch P provides the necessary information. As shown in Appendix 2, $\tau(x'_{\mathrm{FP}})$ is equal to the quantity $\tau(x_{\mathrm{feet,lp}})$, which was measured in the experiment. Furthermore, this relationship is independent of head-bobbing. Therefore, throughout the head-bob cycle, the optic variables $\tau(x'_{\mathrm{FP}})$ and $\dot{\tau}(x'_{\mathrm{FP}})$ continuously specify the physical variables $\tau(x_{\mathrm{feet,lp}})$ and $\dot{\tau}(x_{\mathrm{feet,lp}})$, which the present results indicate govern braking and foot extension during landing flight.

General implications of tau

The tau function of distance to a surface, $\tau(x)$, is apparently used by a number of species for controlling timing during approach – not only under constant approach speed, where $\tau(x)$ gives a precise measure of time-to-contact, but also under changing speed (as in the present study), where $\tau(x)$ provides a first-order estimate of time-to-contact. There is, for example, evidence that $\tau(x)$, registered visually, is used by gannets to trigger streamlining when plunge-diving into the sea (Lee and Reddish, 1981) and by humans to time shock-absorption when landing from a fall (Sidaway *et al.* 1989) and to time the hitting of a dropping ball (Lee *et al.* 1983).

Thus, $\tau(x)$ is potentially a powerful variable for controlling approach to a destination. It provides valuable information for timing preparatory actions like leg extension and for regulating speed of approach. Furthermore, $\tau(x)$ is of such a simple form that it could be registered by a variety of sensory means. The only requirement is for a sensory variable S that is a power function of distance x to the destination (i.e. $S=kx^{\alpha}$, where k and α are constants). Given such a sensory variable, $\tau(x)$ is given simply by the value of $\alpha\tau(S)$. [The proof is straightforward: if $S=kx^{\alpha}$ then, differentiating with respect to time, $\dot{S}=k\alpha x^{\alpha-1}$. Hence, $\tau(S)=S/\dot{S}=(1/\alpha)x/\dot{x}=(1/\alpha)\tau(x)$; i.e. $\tau(x)=\alpha\tau(S)$.]

As an example from a non-visual modality, echolocating bats also appear to control their deceleration when approaching a surface by keeping $\dot{\tau}(x)$ constant (Lee *et al.* 1992*a*). There are two sensory variables that are power functions of distance which bats might use for this purpose: echo-delay and intensity of echo.

$\tau(x)$ might also be used by electrolocating fish. A nearby object at a distance x from the fish distorts the electric field generated by the fish around its body and induces a change S in the transepidermal voltage on the fish which appears to be a power function of distance, the estimate being $S=kx^{-1.7}$ (Bastian, 1986). Because k varies with the conductivity and size of the object, S cannot, by itself, specify the distance x of the object. $\tau(x)$, however, is specified by $\tau(x)=-1.7\tau(S)$.

Finally, it may be noted that controlling approach using $\tau(x)$ is not restricted to a linear approach. Somersaulters, for example, landing upright on their feet appear to control their angular speed to the destination upright by keeping $\dot{\tau}(x)$ constant, where here x is the angular distance from the destination (Lee *et al.* 1992*b*).

Appendix 1: theory of control of speed of approach

The theory which applies to approach along any dimension, will be illustrated by the linear approach of an animal to a surface (Fig. 6A). The point on the surface being approached is considered the origin O and at time t the animal A has coordinate x (arbitrarily taken to be less than zero) and is approaching O at speed $\dot{x}$ and acceleration $\ddot{x}$ ($\dot{x}$ and $\ddot{x}$ denote the first and second derivatives of x with respect to time). The *tau function* of x is defined as x divided by its rate of change over time ($\dot{x}$):

$$\tau(x) = x/\dot{x}. \tag{A1}$$

$-\tau(x)$ is the time it would take the animal to reach O if it were to continue at a constant approach speed $\dot{x}$ The rate of change of $\tau(x)$ [$=\dot{\tau}(x)$] provides information for controlling speed of approach. Differentiating equation A1:

$$\dot{\tau}(x) = 1 - x\ddot{x}/\dot{x}^2. \tag{A2}$$

It is clear from this equation that, during approach to O (i.e. $x<0$ and $\dot{x}>0$): $\dot{\tau}(x)>1$ implies that the animal is accelerating (i.e. $\ddot{x}>0$) and time-to-contact is less than $-\tau(x)$; $\dot{\tau}(x)=1$ implies that the animal is moving at constant velocity (i.e. $\ddot{x}=0$) and time-to-contact$=-\tau(x)$; $\dot{\tau}(x)<1$ implies that the animal is decelerating (i.e. $\ddot{x}<0$) and time-to-contact is greater than $-\tau(x)$.

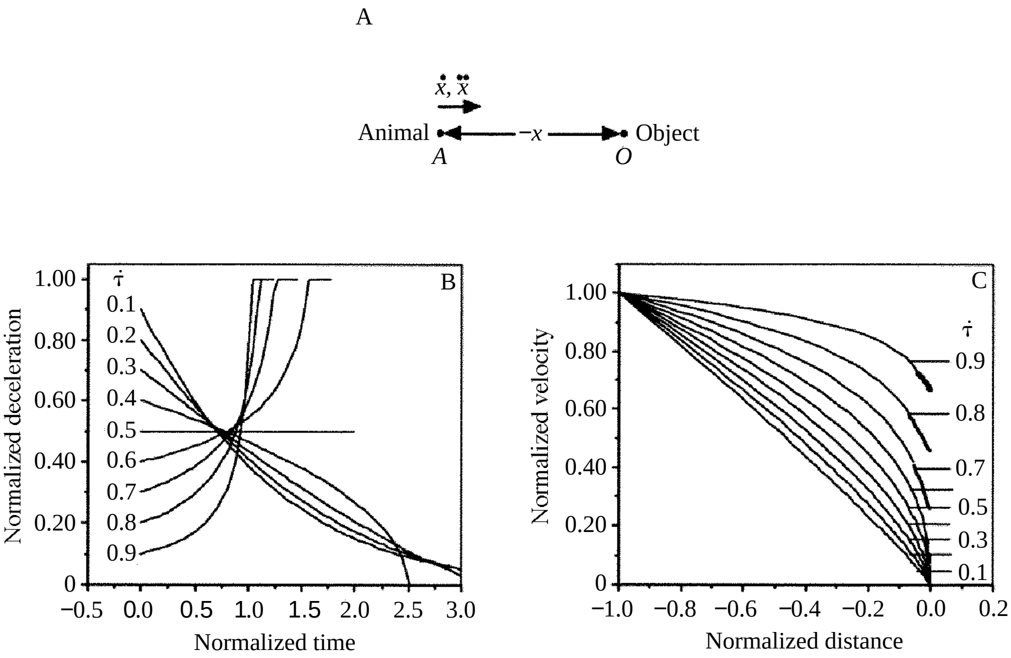

Fig. 6. An illustration of the theory of control of speed of approach. (A) Notation for linear approach. At time t animal has coordinate x (<0) and is approaching its destination with speed $\dot{x}$ (>0) and acceleration $\ddot{x}$ ($\dot{x}=\mathrm{d}x/\mathrm{d}t$, $\ddot{x}=\mathrm{d}^2x/\mathrm{d}t^2$). Tau function of $x=\tau(x)=x/\dot{x}$. Rate of change of $\tau(x)=\dot{\tau}(x)=\dot{\tau}$. (B) Curves showing how normalized deceleration would change over time if approach were controlled by keeping $\dot{\tau}$ constant at the different values shown (see Appendix 1 for equations of curves). (C) Corresponding curves for normalized speed of approach. If $0<\dot{\tau}<0.5$, normalized deceleration monotonically decreases (curves for $\dot{\tau}$=0.1–0.4 in B) and animal stops just as destination is reached (corresponding curves in C). If $\dot{\tau}$=0.5, deceleration is constant (horizontal line in B) and again animal stops just as destination is reached ($\dot{\tau}$=0.5 line in C). If $0.5<\dot{\tau}<1$, deceleration increases monotonically, as shown by curves for $\dot{\tau}$=0.6–0.9 in B; horizontal lines at top of curves correspond to reaching a deceleration ceiling. Thus, animal reaches destination with a certain reduced speed (curves for $\dot{\tau}$=0.6–0.9 in C) and makes controlled collision with it.

Constant deceleration approach

Suppose the animal is decelerating towards O with *constant* deceleration $-\ddot{x}$ (>0). Then the stopping distance from approach speed $\dot{x}$ will be $-\dot{x}^2/(2\ddot{x})$. Therefore, the animal will stop short of O, providing $-\dot{x}^2/(2\ddot{x})<-x$, i.e. providing $x\ddot{x}/\dot{x}^2>0.5$. Thus, applying equation A2, the condition for stopping short is:

$$\dot{\tau}(x) < 0.5. \qquad \text{(A3)}$$

If $\dot{\tau}(x)=0.5$, the animal will stop right at O.

Thus, though control of braking might appear to require information about the current distance from the destination, and about the current speed and deceleration of approach, none of this information is strictly necessary. To avoid collision, it is sufficient to register the value of $\dot{\tau}(x)$, adjust braking so that $\dot{\tau}(x)\leqslant 0.5$ and then keep braking constant.

Application of this constant-braking procedure will necessarily result in $\dot{\tau}(x)$ getting progressively smaller over time and the animal stopping short of the destination [except if $\dot{\tau}(x)=0.5$, when $\dot{\tau}(x)$ will stay constant and the animal will stop at the destination]. Conversely, if deceleration is kept constant when $\dot{\tau}(x)$ is greater than 0.5, then $\dot{\tau}(x)$ will get progressively larger over time and the animal will collide with the destination.

Constant $\dot{\tau}(x)$ *approach*

To *stop at* a destination it is sufficient to adjust braking so that $\dot{\tau}(x)$ stays constant at a value k, $0<k\leqslant 0.5$. The equations of motion resulting from following this procedure are obtained by integrating equation A2 and substituting the constant value k for $\dot{\tau}(x)$. The equations of motion are:

$$x/x_0 = (1 + kt/\tau_0)^{(1/k)}, \tag{A4}$$

$$\dot{x}/\dot{x}_0 = (1 + kt/\tau_0)^{(1/k)-1}, \tag{A5}$$

$$\ddot{x}(x_0/\dot{x}_0{}^2) = (1 - k)(1 + kt/\tau_0)^{(1/k)-2}, \tag{A6}$$

where $-x_0$, $\dot{x}_0$, $-\ddot{x}_0$ are, respectively, the animal's distance from the destination and its speed and deceleration of approach at time $t=0$. $\tau_0=x_0/\dot{x}_0$.

We assume the animal is moving towards the destination O at time $t=0$; i.e. $x_0<0$ and $\dot{x}_0>0$. Therefore $\tau_0<0$. Hence, from equation A4, x/x_0 will decrease over time, i.e. the animal will continue to approach O. [If the animal were moving away at $t=0$, then by keeping $\dot{\tau}(x)=k$ it would move away from O.] Equations A4–A6 may then be normalized by writing:

normalized distance = (distance from destination)/(initial distance) = $\dot{x}_n = \dot{x}/\dot{x}_0$,

normalized speed = (speed)/(initial speed) = $\dot{x}_n = \dot{x}/\dot{x}_0$,

normalized time = time/(initial time-to-contact with destination under constant speed) = $t_n = -t/\tau_0$,

normalized deceleration = deceleration/(twice constant deceleration needed to stop at destination) $=\ddot{x}_n = \ddot{x}(x_0/\dot{x}_0{}^2)$.

The normalized equations of motion are:

$$x_n = (1 - kt_n)^{(1/k)}, \tag{A7}$$

$$\dot{x}_n = (1 - kt_n)^{(1/k)-1}, \tag{A8}$$

$$\ddot{x}_n = (1 - k)(1 - kt_n)^{(1/k)-2}, \tag{A9}$$

where normalized time to reach destination is $1/k$.

Following the 'stop-at' procedure of keeping $\dot{\tau}(x)$ constant at a value of k, $0<k\leqslant 0.5$, requires steadily slackening off the brakes as the destination is approached (except for $k=0.5$, when deceleration is constant). This is because the exponent $(1/k)-2$ in equation A9 is positive. How deceleration falls off is shown in Fig. 6B by the lines (derived from equation A9) for $\dot{\tau}(x)=0.1$–0.4. In Fig. 6C, the lines for $\dot{\tau}(x)=0.1$–0.4 (derived from

equations A7 and A8) show how speed of approach decreases to zero as the destination is approached.

Equations A7–A9 also describe the motion of the animal which would result from keeping $\dot{\tau}(x)$ constant at a value of k, $0.5<k<1$. In this case, the exponent in equation A9 is negative. This means that braking has to get progressively *harder* as the destination is approached. Moreover, stopping at the destination in this way theoretically requires reaching infinite braking force. A realistic procedure – which we will call the *controlled-collision* procedure – is to keep $\dot{\tau}(x)$ constant at a value between 0.5 and 1.0 until maximum braking power is reached, and then maintain this braking force. This would result in the animal colliding with the destination but in a controlled way. In Fig. 6B, the curves for $\dot{\tau}(x)=0.6$–0.9 (derived from equation A9) show how deceleration builds up when following the controlled-collision procedure; the horizontal lines at the top of the curves correspond to maintaining, up to collision, a constant maximum normalized deceleration of unity. How normalized speed of approach decreases as a result of these deceleration patterns is shown by the corresponding curves in Fig. 6C (the thicker lines at the end of the curves correspond to the horizontal lines on the deceleration curves in Fig. 6B).

The above results are summarized in Fig. 1C.

Appendix 2: optic information for landing

Fig. 5 shows a schematic eye of a pigeon flying to a perch and bobbing its head. The nodal point of the lens is at E and the flat ‘retina’ is parallel to the instantaneous direction of travel of the bird (for further details, see Discussion). P is a point on the perch to which the bird is flying and F is the point in the pigeon’s body space which the centre of the foot occupies when it is stretched forward to strike the perch in landing. On the retina, the optic projection (real or virtual) of F is F', and the optic projection of P is P'. Fig. 5 shows F on a course that will pass above P. Other courses might pass below P or directly towards P, which is the pigeon’s aim. The different types of course are optically specified by events on the ‘retina’ as follows. From similar triangles:

$$x_{\mathrm{EF}} = x'_{\mathrm{EF}} y_{\mathrm{EF}}, \tag{A10}$$

$$x_{\mathrm{EF}} + x_{\mathrm{FP}} = (x'_{\mathrm{EF}} + x'_{\mathrm{FP}}) y_{\mathrm{EP}}. \tag{A11}$$

Differentiating each of these equations twice with respect to time:

$$\ddot{x}_{\mathrm{EF}} = \ddot{x}'_{\mathrm{EF}} y_{\mathrm{EF}}, \tag{A12}$$

$$\ddot{x}_{\mathrm{EF}} + \ddot{x}_{\mathrm{FP}} = (\ddot{x}'_{\mathrm{EF}} + \ddot{x}'_{\mathrm{FP}}) y_{\mathrm{EP}}. \tag{A13}$$

When the head is bobbing, the acceleration $\ddot{x}_{\mathrm{EF}}$ of the eye relative to the foot reaches about $6\boldsymbol{g}$ and is generally large compared with the acceleration $\ddot{x}_{\mathrm{FP}}$ of the foot relative to the perch. Therefore, ignoring $\ddot{x}_{\mathrm{FP}}$ in equation A13:

$$\ddot{x}_{\mathrm{EF}} = (\ddot{x}'_{\mathrm{EF}} + \ddot{x}'_{\mathrm{FP}}) y_{\mathrm{EP}}. \tag{A14}$$

Hence, from equations A12 and A14:

$$y_{\mathrm{EF}}/y_{\mathrm{EP}} = 1 + (\ddot{x}'_{\mathrm{FP}}/\ddot{x}'_{\mathrm{EF}}). \tag{A15}$$

Thus, assuming that $|\ddot{x}'_{FP}|<|\ddot{x}'_{EF}|$, the position of the perch relative to the flight path of the foot is optically specified as follows. If $\ddot{x}'_{FP}/\ddot{x}'_{EF}<0$ (i.e. $\ddot{x}'_{FP}$ and $\ddot{x}'_{EF}$ have opposite signs), then $y_{EF}<y_{EP}$, i.e. the perch is below the flight path. If $\ddot{x}'_{FP}/\ddot{x}'_{EF}=0$, then $y_{EF}=y_{EP}$, i.e. the perch is on the flight path. If $\ddot{x}'_{FP}/\ddot{x}'_{EF}>0$ (i.e. $\ddot{x}'_{FP}$ and $\ddot{x}'_{EF}$ have the same sign), then $y_{EF}>y_{EP}$, i.e. the perch is above the flight path.

Thus, for a pigeon to steer its feet in the direction of the perch it is sufficient to regulate its flight until $\ddot{x}'_{FP}=0$. If at any time $\ddot{x}'_{FP}$ is not equal to 0 then (a) if $\ddot{x}'_{FP}$ is of the opposite sign to $\ddot{x}'_{EF}$ the flight path needs to be raised and (b) if they are of the same sign the flight path needs to be lowered.

As regards the information for controlling braking, when foot point *F* is on course for the perch, then $y_{EP}=y_{EF}$, and so from equations A10 and A11:

$$x_{FP} = x'_{FP}y_{EF}\,. \tag{A16}$$

Differentiating with respect to time:

$$\dot{x}_{FP} = \dot{x}'_{FP}y_{EF}\,. \tag{A17}$$

Dividing equations A16 and A17:

$$x_{FP}/\dot{x}_{FP} = x'_{FP}/\dot{x}'_{FP}. \tag{A18}$$

That is:

$$\tau(x_{FP}) = \tau(x'_{FP}) \tag{A19}$$

and so

$$\dot{\tau}(x_{FP}) = \dot{\tau}(x'_{FP}). \tag{A20}$$

Since *F* is the point in the pigeon’s body space which the centre of the foot occupies when it is stretched forward to strike the perch in landing, $\tau(x_{FP})$ equals the quantity $\tau(x_{feet,lp})$ measured in the experiment. Thus, from equation A20, $\tau(x_{feet,lp})$ is optically specified by:

$$\tau(x_{feet,lp}) = \tau(x'_{FP}). \tag{A21}$$

It will be noted that the values of the optical quantities $\tau(x'_{FP})$ and $\dot{\tau}(x'_{FP})$, which specify $\tau(x_{feet,lp})$ and $\dot{\tau}(x_{feet,lp})$ and hence provide information for controlling braking, are unaffected by head-bobbing.

The research was supported by a grant from the US Air Force European Office of Aerospace Research and Development to D.N.L. M.N.O.D. was supported by a Medical Research Council studentship.

References

BASTIAN, J. (1986). Electrolocation: behavior, anatomy and physiology. In *Electroreception* (ed T. H. Bullock and W. Heiligenberg), pp. 577–612. New York: Wiley.

BOOTSMA, R. J. AND VAN WIERINGEN, P. W. C. (1990). Timing an attacking forehand drive in table tennis. *J. exp. Psych: Human Perception and Performance* **16**, 21–29.

BORST, A. AND BAHDE, S. (1988). Spatio-temporal integration of motion. *Naturwissenschaften* **75**, 265–267.

DAVIES, M. N. O. AND GREEN, P. R. (1988). Head-bobbing during walking, running and flying: relative motion perception in the pigeon. *J. exp. Biol.* **138**, 71–91.

DAVIES, M. N. O. AND GREEN, P. R. (1990). Flow-field variables trigger landing in hawk but not in pigeons. *Naturwissenschaften* **77**, 142–144.

DAVIES, M. N. O. AND GREEN, P. R. (1991). The adaptability of visuomotor control in the pigeon during landing flight. *Zool. Jahrbüch.* **95**, 331–338.

KIM, N. G., TURVEY, M. T. AND CARELLO, C.(1992). Optical information about the severity of upcoming contacts. *J. exp. Psych: Human Perception and Performance* (in press).

LACQUANITI, F. AND MAIOLO, C. (1989). The role of preparation in tuning anticipatory and reflex responses during catching. *J. Neurosci.* **9**, 134–148.

LEE, D. N. (1976). A theory of visual control of braking based on information about time-to-collision. *Perception* **5**, 437–459.

LEE, D. N. (1980). The optic flow field: the foundation of vision. *Phil. Trans. R. Soc. Lond. B* **290**, 169–179.

LEE, D. N., LISHMAN, J. R. AND ANDTHOMSON, J. A. (1982). Visual regulation of gait in long jumping. *J. exp. Psych: Human Perception and Performance.* **8**, 448–459.

LEE, D. N. AND REDDISH, P. E. (1981). Plummeting gannets: a paradigm of ecological optics. *Nature* **293**, 293–294.

LEE, D. N., REDDISH, P. E. AND RAND, D. T. (1991). Aerial docking by hummingbirds. *Naturwissenschaften* **78**, 526–527.

LEE, D. N., VAN DER WEEL, F. R., HITCHCOCK, T., MATEJOWSKY, E. AND PETTIGREW, J. D. (1992*a*). Common principle of guidance by echolocation and vision. *J. comp. Physiol.* A **171**, 563–571.

LEE, D. N. AND YOUNG, D. S.(1986). Gearing action to the environment. In *Generation and Modulation of Action Patterns* (ed. H. Heuer and C. Fromm), pp. 217–230. Heidelberg: Springer Verlag.

LEE, D. N., YOUNG, D. S., REDDISH, P. E., LOUGH, S. AND CLAYTON, T. M. H. (1983). Visual timing in hitting an accelerating ball. *Q. Jl exp. Psych.* **35**A, 333–346.

LEE, D. N., YOUNG, D. S. AND REWT, D. (1992*b*). How do sommersaulters land on their feet? *J. exp. Psych: Human Perception and Performance* **18**, 1195–1202.

SAVELSBERGH, G. J. P., WHITING, H. T. A. AND BOOTSMA, R. J. (1991). Grasping 'tau'. *J. exp. Psych: Human Perception and Performance*, **17**, 315–322.

SCHIFF, W. AND DETWILER, M. L.(1979). Information used in judging impending collision. *Perception* **8**, 647–658.

SIDAWAY, B., MCNITT-GRAY, J. AND DAVIS, G. (1989). Visual timing of muscle preactivation in preparation for landing. *Ecol. Psych.* **1**, 253–264.

TODD, J. T. (1981). Visual information about moving objects. *J. exp. Psych: Human Perception and Performance* **7**, 795–810.

TRESILIAN, J. R. (1990). Perceptual information for the timing of interceptive action. *Perception* **19**, 223–239.

WAGNER, H.(1982). Flow-field variables trigger landing in flies. *Nature* **297**, 147–148.

WARREN, W. H., YOUNG, D. S. AND LEE, D. N.(1986). Visual control of step length during running over irregular terrain. *J. exp. Psych: Human Perception and Performance* **12**, 259–266.

WOOD, G. A. (1982). Data smoothing and differentiation procedures in biomechanics. *Ex. Sport Sci. Rev.* **10**, 308–362.