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## Plummeting gannets: a paradigm of ecological optics

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Getting around the environment and doing things requires precise timing of body movements. Moreover, there is often little time available to pick up the visual information to organize the action. Consider, for instance, a batsman hitting a fast bowler or a bird alighting on a twig swaying in the wind. The visual and motor systems evidently work in close harmony, vision rapidly and directly providing the information for controlling the action. Here, we present evidence in support of a theory to explain how actions are visually timed. The evidence derives from a film analysis of the spectacular plunge dive of one of Britain's largest seabirds, the gannet (*Sula bassana*).

The theory is based on an analysis of the visual input considered as an optic flow field<sup>1,2</sup>. When the organism is moving towards a surface, or an object is approaching, the time-to-contact under constant closing velocity is specified by a simple parameter,  $\tau$ , of the optic flow field (see Fig. 1). The theory can explain, for instance, rapid timing of actions in ball games and how long jumpers regulate the cadence of their strides in zeroing in for take-off<sup>3,4</sup>. But what if closing velocity is not constant? Can the theory also explain timing of actions in conditions of acceleration?

Watching gannets plunge diving near the Bass Rock in the Firth of Forth, it occurred to us that here was a good test for the theory. The dive is a beautiful example of finely timed locomotor activity. On sighting fish, the bird plummets down into the water from heights of up to 30 m, reaching speeds of up to 24 m s<sup>-1</sup> (54 m.p.h.). It first quickly assumes a swept-back-wing posture (Fig. 2a–c), which allows steering. Then, when only a split second from the water, it rapidly stretches its wings right back for a spearhead entry (Fig. 2d).

The gannet has to time its streamlining very precisely to avoid injury and so needs to keep track of its time-to-contact with the water. As this is a function of its height, velocity and acceleration, it might at first seem that the bird needs to monitor these three variables and compute the time-to-contact from them. However, it could control its timing in a simpler and more direct way by using the optical parameter  $\tau$  (Fig. 1) which specifies time-to-contact under constant closing velocity.

We need simply consider the vertical component of the gannet's movement. If it starts from height  $Z_0$  with zero velocity and dives with a constant acceleration  $A$  (assuming air resistance negligible over the speed range), then after time  $t$  its height  $Z(t)$  and velocity  $V(t)$  will be  $Z(t) = Z_0 - At^2/2$  and  $V(t) = At$ , and so the optical parameter  $\tau(t)$ , which specifies  $Z(t)/V(t)$ , will have the value

$$\tau(t) = (t_d^2 - t^2)/2t$$

where  $t_d = \sqrt{2Z_0/A}$  = duration of dive. Thus, the time-to-

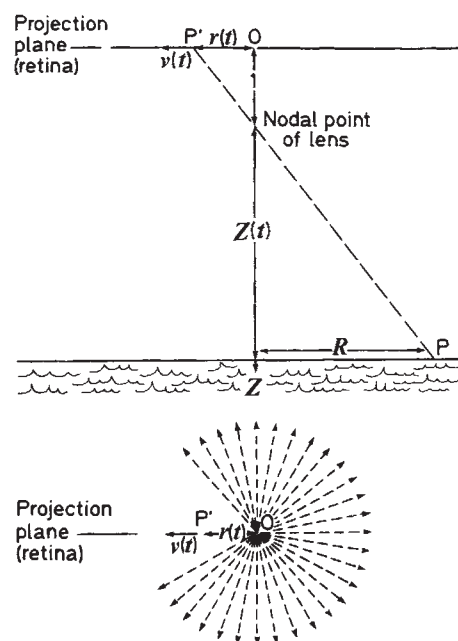


Fig. 1 How time-to-contact is specified in the optic flow field. The schematic eye is, at time  $t$ , at height  $Z(t)$  and moving vertically downward with velocity  $V(t)$  towards the water surface. Light reflected from the surface texture elements (for example, ripples) passes through the nodal point of the lens and projects an expanding optic flow pattern on to the retina. Considering an arbitrary texture element  $P$  and its moving image  $P'$ , then from similar triangles:  $Z(t)/R = 1/r(t)$ . Differentiating with respect to time:  $V(t)/R = v(t)/r(t)^2$ . Finally, eliminating  $R$ ,  $Z(t)/V(t) = r(t)/v(t) = \tau(t)$ ; that is, the time-to-contact under constant closing velocity is specified by the optical parameter  $\tau(t)$ . The optical geometry is similar for a slanting dive.

contact with the water is given by

$$\text{time-to-contact} = t_d - t = \tau(t) + t_d - \sqrt{\tau(t)^2 + t_d^2}$$

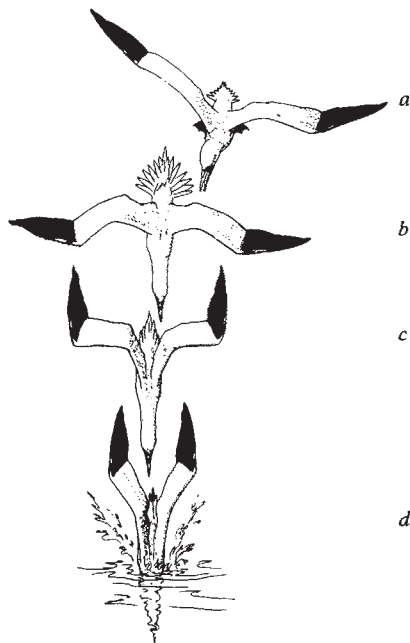
Now, although the optical parameter  $\tau(t)$  does not alone precisely specify the time-to-contact, it could form the basis of a simple heuristic strategy. Suppose the gannet were to start streamlining an initiation time  $t_i$  after detecting that  $\tau(t)$  had reached a margin value  $\tau_m$ . It would therefore start when its time-to-contact with water was  $t_c$ , where

$$t_c = \tau_m + t_d - \sqrt{\tau_m^2 + t_d^2} - t_i \quad (1)$$

Figure 3 plots this equation for a particular pair of values of  $\tau_m$  and  $t_i$ . It illustrates how following the ' $\tau$  strategy' would, in general, result in  $t_c$  increasing with  $t_d$ . Thus, the bird would have more time to streamline itself the longer its dive: the greater the risk of injury the larger the margin allowed for error.

By way of contrast, consider other strategies the bird might use and the form of the  $t_c \times t_d$  curves that would result. First, suppose it could actually detect the time-to-contact and that it started streamlining when it reached a margin value; then the  $t_c \times t_d$  graph would be a level line. Second, suppose it started streamlining when it reached a certain height. It would then have less time to prepare for entry the longer its dive, because it would be travelling faster;  $t_c$  would decrease as  $t_d$  increased. Finally, suppose it started streamlining either at reaching a certain (vertical) velocity or, which is mathematically equivalent, at a constant time  $t_s$  after starting the dive. The prediction would then be  $t_c = t_d - t_s$ ; that is,  $t_c$  would increase linearly with  $t_d$ , the graph having a 45° slope.

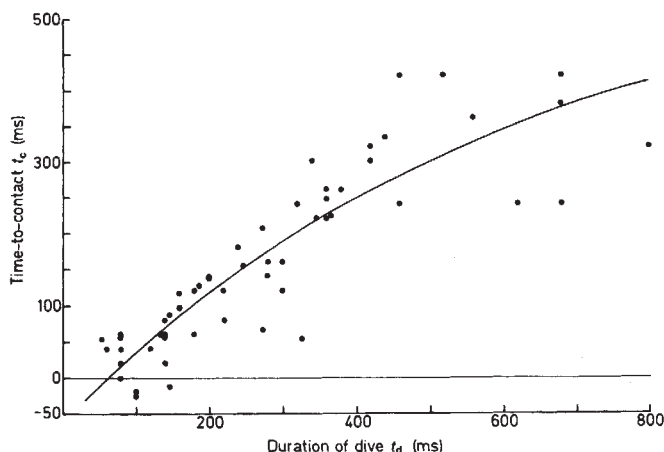
To test between the hypothetical strategies, we used films of dives to measure how  $t_c$  varied with  $t_d$ . The films were shot from the stern of a trawler, fish having been thrown overboard to entice the gannets to display their skill. Their dives were consequently relatively short compared with those when they



**Fig. 2** Wing positions of diving gannet, *Sula bassana* (length ~0.9 m, wingspan 1.7 m). Illustration by John Busby. (Reprinted from ref. 7, courtesy of the author and publishers.)

are preying on a deep shoal of fish. We analysed 55 dives filmed at 50 f.p.s. or 150 f.p.s.

The results (Fig. 3) favour the  $\tau$  strategy. The theoretical curve is the best-fitting member of the family represented by equation (1). It was computed minimizing the r.m.s. distance of the points from the curve; the minimized r.m.s. error was 49 ms. The birds were clearly not streamlining at a constant time-to-contact or at a constant height; nor do the data seem to follow a 45° line as predicted by the constant velocity and constant time-from-start strategies. Indeed, those strategies would make little sense for high dives because they would result in the birds maintaining steering capability for only short fractions of their dives. Clearly, strategies entailing detection of both height and velocity and subsequent computation can be formulated to fit the data. However, such strategies lack the simplicity of the  $\tau$  strategy. Furthermore, the birds would probably not be able to detect their height and velocity with sufficient accuracy, given the very small degree of binocular parallax and the absence of invariant features in their field of view to furnish a spatial metric<sup>2</sup>.



**Fig. 3** How the time before contact when gannets start streamlining increases with the duration of the dive following the predicted curve of equation (1). Occasionally, streamlining was started after the head had entered the water ( $t_c$  negative), but it was invariably completed before submersion.

The parameter values of the curve in Fig. 3 provide measures of the average performance of the birds:  $t_i$  = action initiation time = 60 ms;  $\tau_m$  = margin value of  $\tau$  = 820 ms. It would be interesting to see whether gannets use the same margin value of  $\tau$  in other activities—for example, in preparing to land on a cliff ledge. In that case, with approach velocity about constant,  $\tau$  actually specifies the time-to-contact.

A further interesting question, of course, is whether people also follow a  $\tau$  strategy in visually timing their actions in conditions of acceleration, as they seem to do in constant velocity conditions<sup>4,5</sup>. We are now investigating the question by analysing performance on two skills: high diving and leaping to punch a dropping ball. There is also evidence suggesting that drivers control their deceleration by means of the optical parameter  $\tau$ , for the time derivative of the parameter specifies whether or not their current braking force is adequate to stop before reaching the obstacle<sup>6</sup>.

It is beginning to appear that the information afforded by this ubiquitous optical parameter is much exploited by visual systems. The information is needed for many activities and is available to any seeing organism.

The gannet film was shot by Hugh Miles. We thank him and the BBC for loaning it to us, and David Young for critical comments. The work was supported by MRC grant G979/194/N.

Received 21 April; accepted 10 July 1981.

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## Regulation of lymphatic contractility by arachidonate metabolites

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The circulation of lymph is apparently controlled partly by the pressure of fluid entering the lymphatic capillaries, aided by external forces such as skeletal muscle contraction and gut peristalsis<sup>1,2</sup>, but lymphatic vessels themselves also contract rhythmically when distended *in vivo* or *in vitro* and this may be of major importance in the propulsion of lymph<sup>3–5</sup>. We have studied the effects of biochemical mediators on isolated sheep and bovine lymphatic segments and on pressure pulses from indwelling lymphatic cannulae and report here that nanomolar concentrations of prostaglandin (PG) H<sub>2</sub> endoperoxide and a stable PGH<sub>2</sub> analogue elicited rhythmic contractions and increased the tone of isolated quiescent lymphatic segments. Some segments showed spontaneous rhythmic activity, and these spontaneous contractions could be inhibited not only by aspirin (a cyclo-oxygenase inhibitor) but also by inhibitors of thromboxane synthase (imidazole and compound UK 37248). The pulsatile pressure changes measured from indwelling lymphatic cannulae in conscious sheep were also suppressed by aspirin or imidazole infused directly into the lymphatic circulation. Our results suggest that endogenous thromboxane production is mainly responsible for spontaneous lymphatic contractions but that PGH<sub>2</sub> also has contractile activity. An unknown product of arachidonate and PGH<sub>2</sub>, which could be formed non-enzymatically, inhibited both spontaneous and induced contractions.

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