

## CHASING WITH A MODEL EYE

By STEPHEN YOUNG

*Department of Pure and Applied Biology, Imperial College, Silwood Park,  
Ascot, Berks SL5 7PY*

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### Summary

1. A simulation model for *Polyphemus* eye movements was based on an open-loop saccadic control system, derived from previous observations of eye movements in response to sinusoidally oscillating targets.
2. The model was checked against new observations of *Polyphemus* eye movements in response to erratically moving targets.
3. It was used to predict eye movements in response to stimulus patterns deduced from an analysis of video-recordings of *Polyphemus* chases.
4. The results show that the system is limited to tracking slow target movements, but that this is consistent with observed chasing behaviour.

### Introduction

#### *Polyphemus anatomy and biology*

*Polyphemus* typically swims head-first and dorsal side upwards, as shown in Fig. 1. The single compound eye is very large relative to the body size, and can move freely within the carapace in both the yawing and pitching planes (i.e. around a vertical axis and a horizontal lateral axis for an animal in the normal swimming position). The eye has a small acute zone, 20° across, just above the horizontal midline in a forward-pointing direction (Nilsson & Odselius, 1983). In a static environment there are occasional large eye movements, up to 60° in amplitude, superimposed on a constant background of small trembling movements. Large eye movements are, however, readily evoked by a small moving target (Young & Taylor, 1987).

#### *Eye movements during chases*

Young & Taylor (1988) have shown, using an analysis of video-recorded *Polyphemus* chases, that visual cues such as target apparent size and direction (relative to the chaser's body axis) have important roles in controlling the chaser's behaviour. Unfortunately, it is not possible to record eye position for a free-swimming *Polyphemus*, but there is strong circumstantial evidence that eye movements must occur during chases. Fig. 2 shows the relationship between the

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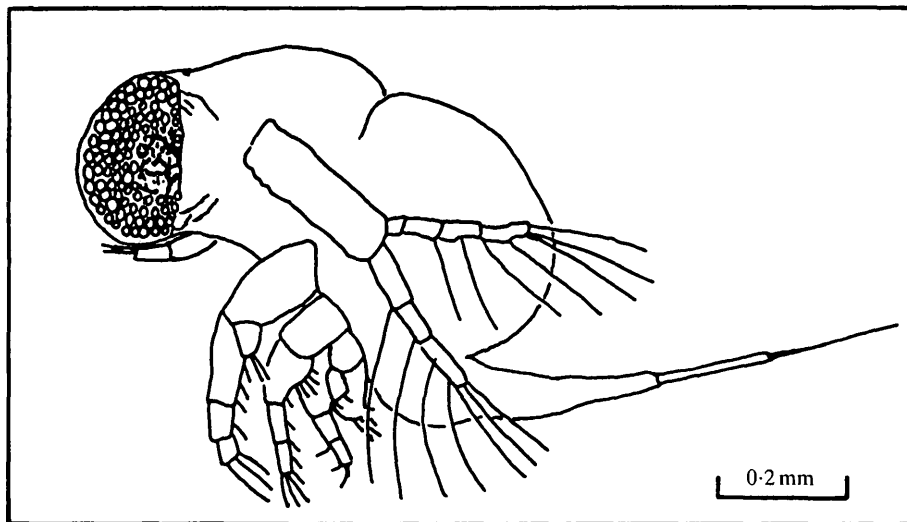


Fig. 1. *Polyphemus* in a typical swimming position, viewed from the side.

angular size of the target and its direction relative to the chaser's body axis at the moment when a chasing *Polyphemus* first responds to the target. On average, the necessary target size increases with increasing deviation from the body axis. This could be explained by the decreasing resolution of the *Polyphemus* eye as the inter-ommatidial angle increases moving around the eye away from the acute zone (solid line, Fig. 2). However, the *minimum* target size needed to evoke a response (lower ends of dotted bars, Fig. 2) remains nearly constant at  $3^\circ$ , no matter how far off-axis the target is detected. In the centre of the acute zone, where the ommatidial spacing is  $2^\circ$ , a  $3^\circ$  target will cover one whole ommatidial field and around one-quarter of each of the six surrounding ones – equivalent to 2.5 ommatidia.  $60^\circ$  off-axis, where the ommatidial fields are  $18^\circ$  across, the same stimulus will cover only 2.7% of an ommatidial field. Thus, it seems likely that when small targets far from the body axis are detected, an eye movement has brought them into the acute zone.

Similarly, during the shadowing phase of chases, when image size and position are crucial inputs for the chaser (Young & Taylor, 1988), the tolerated range of target deviations from the body axis direction averages ( $\pm$ s.e.)  $44.3 \pm 4.1^\circ$ , over twice the extent of the acute zone. Once again, it seems probable that eye movements are used to keep the target image in the acute region of the eye.

#### *Evoked eye movements*

A *Polyphemus* eye can sometimes be seen to track a moving target. To evoke this response, the target must subtend at least  $3^\circ$  at the animal's eye, and its image must enter the central region of the eye.

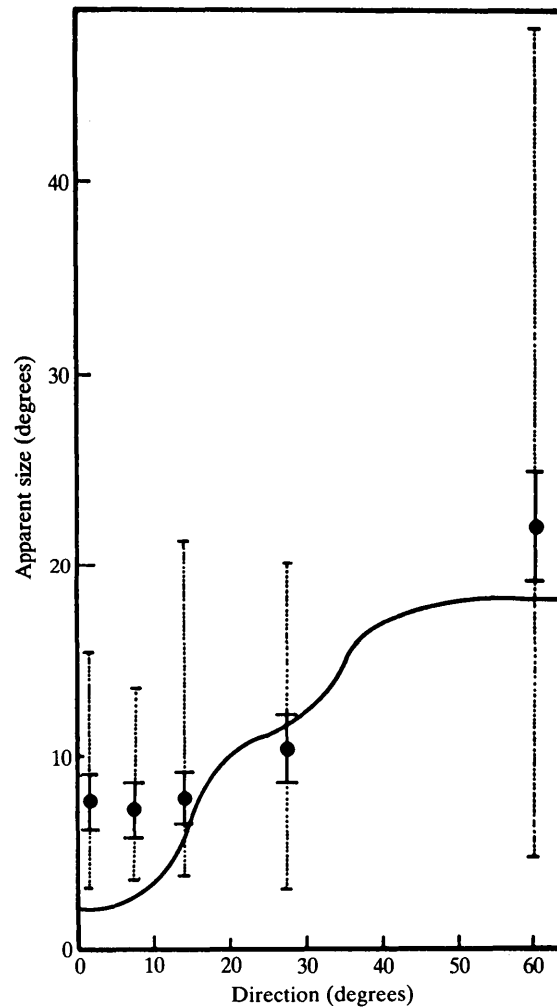


Fig. 2. Apparent size (angular subtense at eye) of target viewed by a chasing *Polyphemus*, plotted against its direction, measured as an angle with respect to the chaser's body axis at the moment of first response. Points are means for each group of values. Solid bars are standard errors, and dotted bars are ranges. The solid line shows how the interommatidial angle (y-axis) changes with angle out from the acute zone (x-axis) for a *Polyphemus* eye. (Data from Nilsson & Odselius, 1983.)

The response is similar whether the target is a dark stripe on a bright background, a bright stripe on a dark background or a single dark/bright edge. Slow-moving targets produce much larger responses than fast-moving ones, but the speed of target movement has very little effect on the speed of eye rotational movement, which is essentially a constant for a given animal. An eye movement begins with a rapid acceleration to the fixed rotation speed ( $S$ ). The extent of the movement is determined by the time during which this steady rotation is maintained ( $R$ ) before an equally rapid stop.

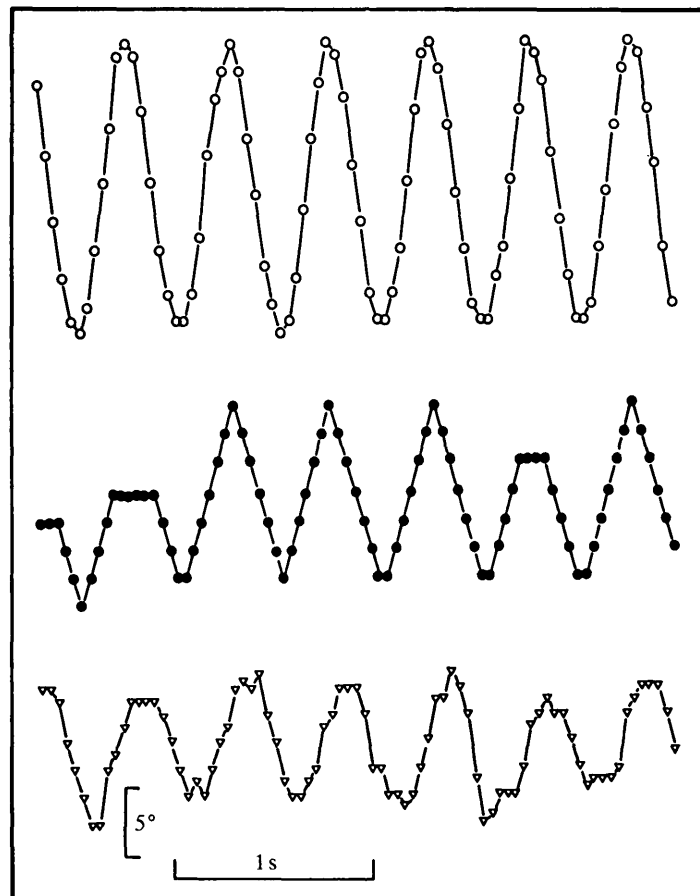


Fig. 3. Typical response of a *Polyphemus* eye (open triangles) to a sinusoidally moving stimulus bar (open circles). The middle trace (solid circles) gives the corresponding output from the model eye.

#### *Response to sinusoidal target oscillations*

Our investigation of this system (Young & Taylor, 1987) used dark vertical stripes,  $6^\circ$  wide, oscillated horizontally along a circular segment centred on the eye. The position of the stripe followed a sinusoidal time course, moving fast past the centre of the eye, and slowing steadily into each reversal of direction (Fig. 3). The target and eye positions were recorded on video for a wide range of frequencies and amplitudes of target oscillation. Analysis of these data revealed an open-loop control system in which the duration of stimulation each time the target image passed through a sensitive region of the eye controlled the extent of a subsequent eye movement. Fig. 4 is an intuitive representation of the proposed mechanism for the way a single stimulus event controls a subsequent eye movement. A hydraulic representation of the complete control system would be more complicated, because the direction of the response always followed the

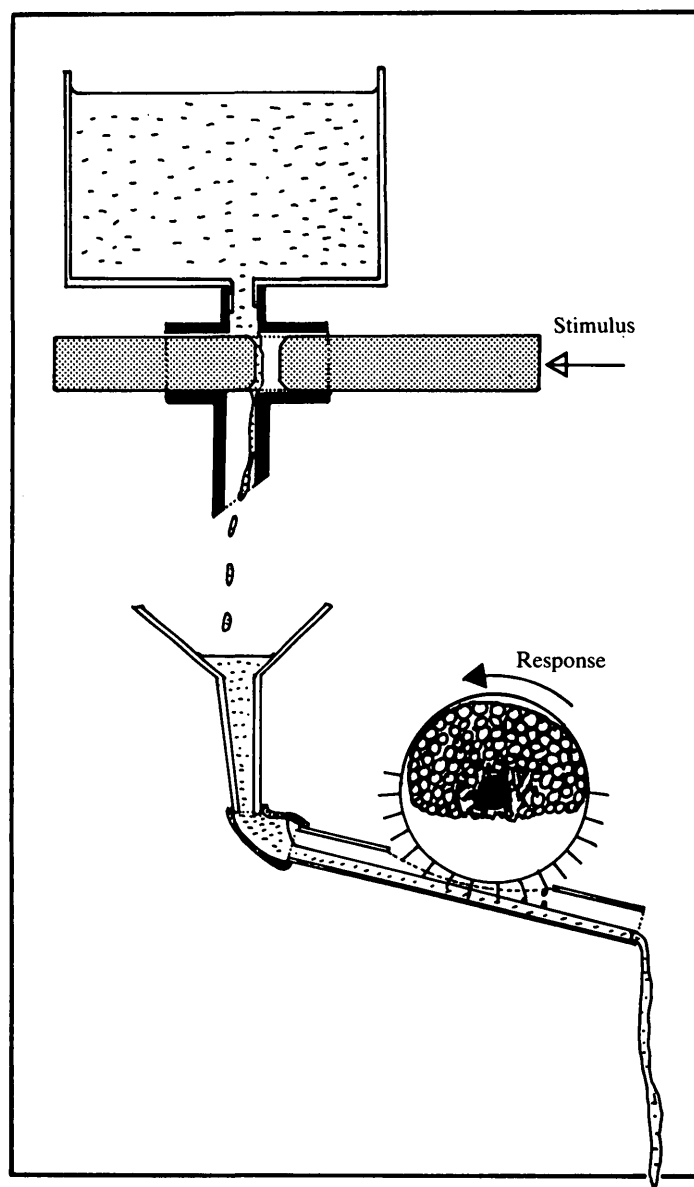


Fig. 4. A hydraulic version for the mechanism controlling a single eye movement.

direction of the stimulus. The latency between the start of a stimulus and of a response was about 60 ms (see Fig. 5E).

In quantitative terms, the duration of an eye movement was logarithmically related to the preceding period ( $t$ ) for which the target image remained in the eye's sensitive zone:

$$R = 53 \cdot 4 \ln(t) - 128 ,$$

where  $R$  and  $t$  are both measured in ms. From this we can deduce that, if a target image entered the sensitive zone  $T$  ms ago, its current rate of contribution to the response is:

$$\frac{dR}{dT} = \frac{53.4}{T}.$$

### Eye movement simulation model

#### *Model specification*

The relationship above can be used to construct a model to simulate the eye movements which would be evoked by an irregularly moving target. The stimulus is specified as a sequential list of angular positions of the target relative to the animal's body axis. The sampling interval is 20 ms, corresponding to a video half-field.

Each sample is evaluated in turn. If the target is within  $\pm 10^\circ$  of the current eye axis position, it is taken to be in the sensitive zone, and will hence be contributing to the length of a subsequent response. The last value of the response timer,  $R(t - 20)$ , is updated. Either:  $R(t) = R(t - 20) + (53.4 \times 20)/T$ , if the target is moving from right to left, or  $R(t) = R(t - 20) - (53.4 \times 20)/T$ , if the target is moving from left to right. The value of  $T$  is then increased by 20 ms. The direction of target movement is assessed relative to the *Polyphemus* body axis. A functioning model cannot be produced using direction of image movement on the eye instead.

The sign of  $R(t)$  determines the direction of the response, and its modulus,  $|R(t)|$  the response duration. If  $R(t) > 0$  and  $T > 60$  (to allow for the response latency – see Fig. 5A for the effects of different values), the eye must move. The movement is always a single fixed step; either clockwise [ $R(t)$  positive] or counter-clockwise [ $R(t)$  negative]. The size of the step is  $(S/50)^\circ$ , where  $S$  is the eye's slew rate, measured in degrees  $s^{-1}$ . Finally,  $R(t)$  is reduced by 20 ms, because 20 ms of movement time have been 'used up'.  $T$  is reset to zero each time the target image re-enters the sensitive zone.

Two parameters need to be set. (a) The slew rate ( $S$ ), for which observed values range between 30 and 60 degrees  $s^{-1}$  (Young & Taylor, 1987). The model needs values at the upper end of this range to work well, probably because the data came from animals which responded strongly to stimulation. It becomes unstable if values larger than 150 degrees  $s^{-1}$  are used. (b) The offset is the initial position of the eye axis on the arbitrary scale used for measuring target position. Eye positions

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Fig. 5. (A) The top trace shows the movement of the stimulus, and the bottom trace a *Polyphemus* eye-movement response. The middle three traces are all generated by the model, with the response latency set to 30, 60 and 120 ms, respectively. The model output is little affected by the value chosen. (B–D) Comparisons of the model output (middle trace), with the real eye (bottom trace) for various stimulus movement patterns (top trace). (E) A similar plot, showing two step-like movements of the target resulting in single, clearly defined responses. A close examination of this eye-movement record yielded the 60 ms estimate of response latency used in the model.

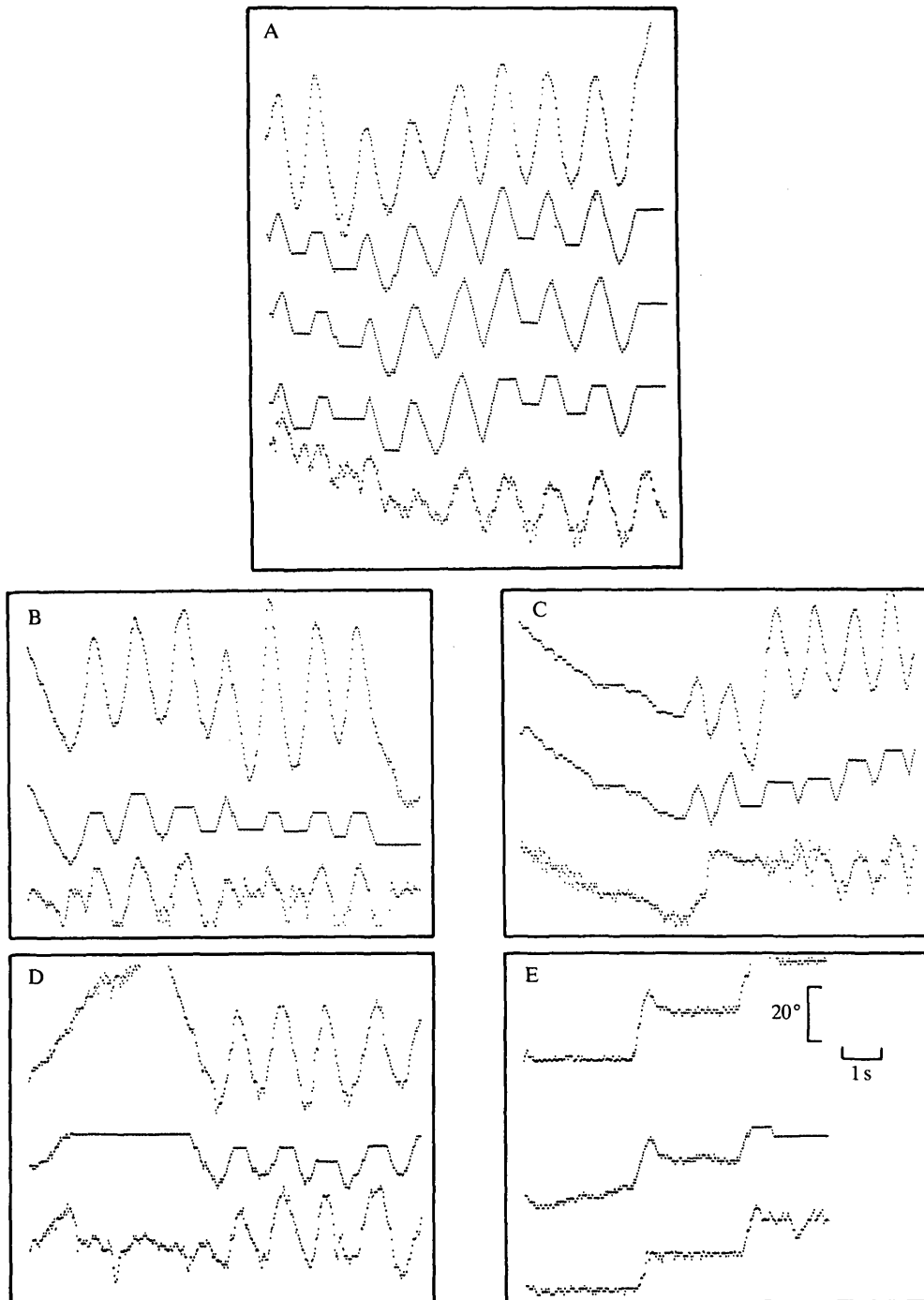


Fig. 5

and stimulus positions were measured on separate angular scales with arbitrary origins, which could be related only by visual inspection of the start frame; as the living eye lacks convenient landmarks, this is only accurate to about  $20^\circ$ . The actual value chosen has a large effect on the model output, and trial and error within the experimentally observed range has been used to produce the results in Fig. 5.

This same problem makes it impossible to delimit the sensitive zone exactly. If a target was introduced so that its image fell at the edge of the eye, it produced no response, and could be moved around the eye until the central zone was reached before any reaction was observed. Attempts to analyse video-recordings of the first response to a stimulus introduced in this way failed to produce satisfactory results. This was partly due to tremor movements masking the beginning of the response, but mainly because it was impossible to judge exactly where on the eye the target's image was falling. The model uses a  $20^\circ$  window centred on the eye axis, assuming the anatomical acute zone is the sensitive zone.

#### *Comparing the model with a real Polyphemus*

Fig. 3 includes a trace generated by the model, showing that output amplitude is correct for a sinusoidal stimulus input. Fig. 5 enables comparison of the responses of both the model and a *Polyphemus* to various irregular stimulus movements. The data were generated by moving a pencil (subtending  $7^\circ$  at the eye) around an immobilized *Polyphemus* in the apparatus described by Young & Taylor (1987). The digitized positions of the pencil from the video-recording were used as the input for the model.

Given that the real eye reverts to erratic low-amplitude tremor in the absence of an evoked response, whereas the model stays steady, the correspondence was reasonably good. Fig. 5E shows both model and eye succeeding in tracking two sudden movements of the stimulus. The first half of the record in Fig. 5D shows that, despite the absence of continuous negative feedback, both model and real eye track a slowly moving target reasonably accurately. Conversely, both lose a faster moving target in the record in Fig. 5C, then start tracking it again when it returns to the sensitive zone. Fig. 5A and 5B are examples of irregularly repetitive large-amplitude target movements, which lead to periods of attenuated response interrupted by snatches of good tracking for both model and real eye.

#### *Chases with the model eye*

Using track data reported in Young & Taylor (1988), we calculated the visual inputs received by the chasing *Polyphemus* during the shadowing phase of three sample chases. Our chase data were digitized at 100-ms intervals, so interpolation was used to generate a list of target positions suitable for the model. Fig. 6 shows the response of the model to these stimuli. The records in Fig. 6B and 6C came from chases leading to contact, and illustrate good eye tracking in the final phases but that shown in Fig. 6A came from a chase which terminated, and shows the eye losing the target just before the chaser peeled off. Fig. 6D shows simulated eye



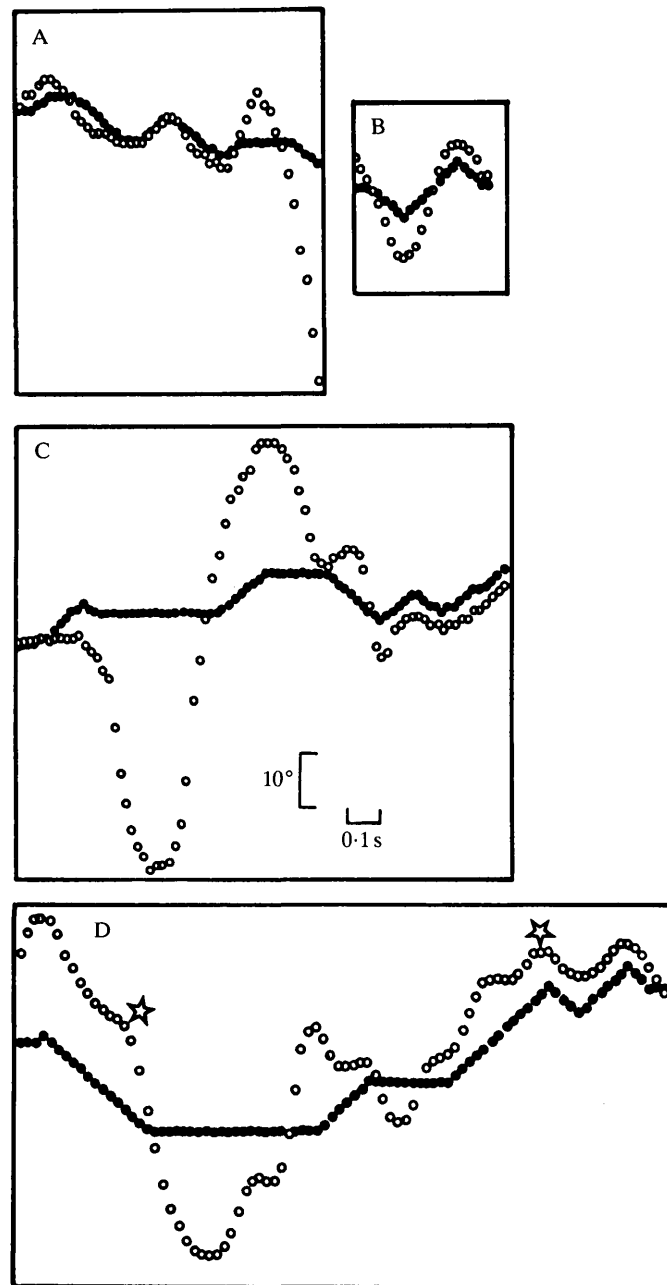


Fig. 6. (A–C) Model eye response (solid circles) to target movements (open circles) generated during the shadowing phases of three *Polyphemus* chases. (D) A similar plot of a simulation of eye movements during a pause in a chase. The period during which the chaser pivots on the spot to keep the target in view is delimited by the two stars.

movements during a pause. The data are from the chase shown in Fig. 1C in Young & Taylor (1988). By the time shadowing commences (after the second star) the target is being accurately tracked.

### Discussion

The basis of the simulation model for *Polyphemus* eye movements proposed here is an open-loop or saccadic system, with the extent of each individual movement pre-determined by a brief input generated as the image of a moving target traverses a sensitive zone on the eye. The sensitive zone needs neurones capable of detecting the presence of a moving target, and of assessing the direction of target movement, so that a sophisticated system of the sort described in insects (Collett & King, 1975) is necessary.

The presence in the model of a timer (T) for the duration of each stimulus does not imply that a *Polyphemus* would need such a device. Its function in the model was to enable the simulation of an adaptational decline in stimulus efficacy with lengthening stimulation. Obviously, this would happen in real time in *Polyphemus*, which would need no clock to regulate the process. This is analogous to the way a car speedometer has an output in miles per hour, although the device does not include any sort of clock.

The core of the model is the response timer (R) which is topped up by stimuli and consumed by responses. The eye must be able to move in two directions, depending on the sense of the stimulus movement, and early versions of the model had two separate timers for the two response directions. The current system uses a single parameter, whose sign controls the direction of the response. Stimulus contributions are added to, or subtracted from, R depending on *their* direction. This works well, and avoids the situation in which the eye receives conflicting instructions from the two separate timers.

The similarities between the outputs of the model and the behaviour of *Polyphemus* eyes in response to erratic stimuli provided non-trivial support for our mechanism, since the model was devised using data from sinusoidally moving targets only. In particular, the model's success in tracking slow-moving targets shows that the ability of a *Polyphemus* to perform the same task is not grounds for rejecting an open-loop control mechanism for eye movements.

The major drawback of the system is the need for large eye movements to be comparatively slow. The model is conspicuously stable, even though it lacks any mechanism to re-centre the eye in the absence of a valid stimulus, provided the slew rate (S) is not increased much above observed levels. With higher slew rates it oscillates wildly, rapidly exceeding a 180° rotation. The visual inputs calculated from chase observations show that rates of change of target direction greatly in excess of maximum eye slew rates are common.

The peculiar features of the *Polyphemus* eye-movement control system – the small sensitive zone, and the absence of continuous visual monitoring of target position – are probably due to the very small number of ommatidia in the eye,

especially when compared with insect eyes. The acute zone has only 25 ommatidia, and peripheral interommatidial angles are about 20° (Nilsson & Odselius, 1983). Thus, peripheral movement detectors would need enormous targets. Even in the acute zone large-scale comparisons across an extended array of receptors are clearly impossible. Thus, in practice, *Polyphemus* need both eye movements and body-axis orientation changes to keep a moving prey in view during a chase.

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