

## Ocular limit cycles induced by delayed retinal feedback

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**Abstract.** Lisberger's and Robinson's models of smooth pursuit predict very different results from altering retinal feedback delay. We have therefore investigated the effects of increasing the retinal feedback time delay in three normal human subjects by means of an artificial feedback paradigm. When additional delays were incorporated into the retinal feedback path a threshold was reached beyond which the eye exhibited sustained self-excited oscillations or "limit cycles". The oscillation period increased linearly (as the added delay was increased) with slopes ranging from 1.41 to 1.6 with zero-delay intercepts of between 212 and 306 ms. Contrary to our experimental findings the Robinson and Lisberger models predict that the plot of oscillation period against added delay should have a slope of 3.4 and 2.7 and an intercept of 479 and 554 ms, respectively. Neither model produced comparable limit cycles, both being unstable at delays greater than 280 ms. Our results imply that the models of smooth pursuit need to incorporate predictive control.

**Key words:** Eye movements – Smooth pursuit models – Smooth pursuit eye movements – Time delays – Human

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### Introduction

The function of smooth pursuit is to keep an object, once located, on or near the fovea (Carpenter 1988). Large retinal errors are first removed by the saccadic system and the smooth pursuit system then seeks to match eye velocity to target velocity. There is a consensus of opinion on several features required of a model of smooth pursuit control. The main input to the controller is believed to be retinal velocity error (difference between target velocity and eye velocity) and the output of the controller is the

pursuit or motor command which acts on eye musculature producing eye movement which in turn affects the retinal velocity error. The system, therefore, acts within an overall negative feedback loop. The negative feedback loop incorporates delays of approximately 90–130 ms that arise from a mixture of sensory processing and motor output delays (Robinson et al. 1986). Viable models of smooth pursuit must therefore also include such delays.

Two broad classes of pursuit models have been described (Fig. 1). The first class is the efference copy, corollary discharge, or "internal model" controllers (Fig. 1a). Such controllers can make use of internal model representations of the eye (Young 1971) and/or of target motion (Pavel 1990). The internal model of the eye receives the pursuit command (efference copy) as input, and thereby recreates an internal estimate of eye velocity. Young et al. (1968) proposed that internal positive feedback of eye velocity could be used to cancel the external negative feedback of eye velocity, effectively leading to feedforward control. In other words, the addition of estimated eye velocity onto retinal slip could be used to recreate target velocity and this could be used to drive the eye. Robinson et al. (1986) have modified the Young hypothesis, to take account of the mismatch in time between the internal feedback loop and the efferent arm of the external (actual) feedback loop, by including a time delay in the internal feedback loop (Fig. 1a). By using an internal model of the eye in a positive feedback loop they were able to prevent the instability problems seen in simple feedback controllers with high gain and substantial feedback delays. The recreation of target velocity via an internal model also enables pursuit to be maintained even when retinal slip is zero; and steady state gains greater than 1 can be achieved. Such gains have occasionally been observed in human pursuit and cannot be explained with simple velocity feedback.

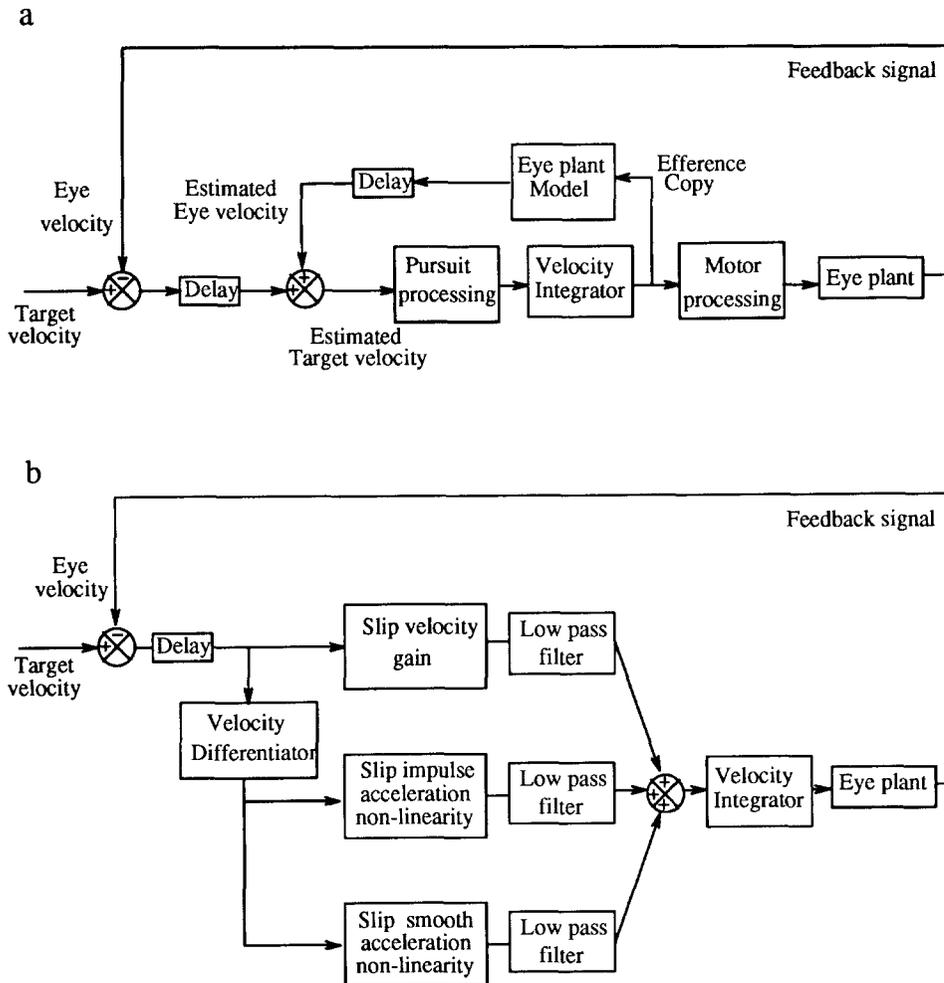
However, three problems exist with such efference copy models; first the efference copy internal models must be accurate in order to estimate target velocity successfully; secondly the internal copy of eye velocity must be delayed by the same amount of time as the external

feedback delay; and lastly, as yet, no eye velocity signals appropriate to be the output of the model have been recorded (Keller and Heinen 1991).

The second class of models are the parallel processing models (Fig. 1b) proposed by Krauzlis and Lisberger (1989), in which there is no internal feedback. Although these models are based on modelling the initial 200 ms of ramp pursuit, they are also able to reproduce pursuit under different conditions. Lisberger's model contains no corollary discharge but instead uses a set of nonlinear parallel pathways which act both on retinal velocity and acceleration errors. The pathways' nonlinearities ensure a speedy initial response while maintaining stability in the steady state. However, efference copy is not used by this model, even though it is known to be present at the cortical level. Neither model makes use of retinal positional error which can evoke smooth pursuit (Grusser 1986).

Deno et al. (1989) have shown that a linear internal feedback model can be reformulated to be a linear parallel feed-forward model and vice versa. Hence linear versions of the Lisberger and the Robinson model can be recast as sub-types of more general classes of model. Thus although conceptually different, one could not determine which model was realistic just by observing the behaviour of the intact oculomotor system.

One way of testing for differences in these models is to test their responses to different feedback time delays. We have investigated the effects of altering the intrinsic time delays in the Lisberger and Robinson models of pursuit. The two models produce different predictions. We have therefore gone on to study the effects of adding additional retinal delays on human oculomotor control. In humans the internal delays cannot be altered directly, but extra delays may be simulated electronically by modifying the position of a target in relation to eye movement signals. We used a variation of the technique of Robinson (1965) and of Collewijn and van der Mark (1972) to delay visual feedback artificially (Deno et al. 1989; Goldreich and Lisberger 1987). The aim was to investigate the effects of such delay changes on the pursuit system. We chose to allow the eye to start off in fixation of a stationary target in preference to a pursuit task, as it allows the study of self-sustained responses uncontaminated by an external stimulus. While it seems likely that fixation and pursuit are controlled by separate systems (Luebke and Robinson 1988; Goldreich et al. 1992), the introduction of a delay that causes oscillations effectively shifts the task from fixation to pursuit. In this series of experiments we have studied this self-generated pursuit. Subsequent to the completion of these experiments, Goldreich et al. (1992)



**Fig. 1a,b.** Schematic diagrams of the two major classes of smooth pursuit model. **a** Robinson's efference copy model, which uses internal feedback to reconstruct target velocity. **b** Lisberger's parallel feed-forward model which uses multiple nonlinear paths acting on both acceleration and velocity error

published a similar series of experiments, using rhesus monkeys. We have compared our human results with those obtained in the monkeys.

## Materials and methods

Three normal human subjects participated in the experiments, two men and one woman. The two male subjects (D.M.W. & R.C.M.) were experienced in both eye-movement recording and oculomotor neurophysiology and were aware of the purpose of the experiments; the third subject (M.A.S.) was naive to the experiments and was not informed of their purpose. Subjects sat in a dimly lit room 30 cm in front of a green, low-persistence oscilloscope screen (Telequipment DM53A) on which a spot target was displayed. The intensity of the target was adjusted so that no perceptible persistence was observed when the target was displaced. The spot could move horizontally across a range of  $13.8^\circ$  centred on the subject's right eye. The movements of the target were controlled by computer with a 12-bit digital-to-analogue converter running at 500 Hz. The subjects were instructed to follow this target as accurately as possible with their right eye; refractive errors of the right eye were corrected with a lens, and the left eye was covered. The head was stabilised using a dental impression bite bar and forehead rest.

## Stimulus presentation

The target spot had no intrinsic movement. In order to incorporate an additional extrinsic time delay of  $T_{\text{ext}}$  milliseconds into the oculomotor feedback loop, the displayed target spot was displaced by the angle through which the eye had moved during the previous  $T_{\text{ext}}$  milliseconds. Therefore if  $E_t$  is the eye's angular position at time  $t$ , the target's angular displacement was  $E_t - E_{t-T_{\text{ext}}}$ . Thus, the difference between current and past eye positions was used to control the target location. By this means movement of the target's image across the retina due to eye movements during the delay period were negated, while after  $T_{\text{ext}}$  the spot would shift across the retina, simulating delayed movement to the new eye position. Normal vision was preserved in the vertical direction.

This procedure places a delay in both the smooth pursuit and saccadic systems. To study the effects of delays on the smooth pursuit system in isolation we detected saccades on-line with a velocity threshold (see below). We have studied the effects of delaying feedback both with and without this velocity threshold.

## Eye position recording

The horizontal angular position of the right eye was monitored using the IRIS infrared reflection system. The maximum resolution of this system is 5 min of arc (Reulen et al. 1988). The eye position signal was sampled by computer with 12-bit resolution at 500 Hz. The signal was then smoothed using a three-point triangular filter. The eye position signal was calibrated at the beginning, middle and end of each experimental session. During calibration, subjects were requested to follow the target as it covered the  $13.8^\circ$  range of the screen in four equal steps (5 calibration points). At each point the subject was required to fixate the stationary target for at least 500 ms; adequate fixation was determined by the range of eye position samples during this period. If the eye moved by more than 2% of the analogue/digital range, or the subject blinked, the target remained at that location until a good fixation was recorded. In order to fit a calibration curve, eye position was then taken as the mean of the middle 150 samples (300 ms) of the 500-ms fixation period. A linear regression was then performed on the five fixation values of eye position against angular displacement of the target. This regression equation was used during subsequent experimental trials to deter-

mine on-line the angular position of the eye. The correlation coefficient for all calibrations was greater than 0.99 and the mean change in regression slope between consecutive calibrations was no greater than 5%.

To prevent the saccadic system from being delayed the eye velocity was thresholded on-line and then integrated, thereby leaving only the smooth pursuit component of the eye movements. The threshold was set at  $50^\circ \text{ s}^{-1}$ ; smooth pursuit velocity in our experiments did not exceed  $40^\circ \text{ s}^{-1}$ . This reconstructed record often showed positional drift because corrective saccades had been removed. To remove this drift prior to analysis a quadratic polynomial was fitted to and then subtracted from each eye position trace.

## Experimental protocol

Each session consisted of 14, randomised, 15-s trials, one at each particular delay. The delay was varied between 0 and 520 ms in 40-ms intervals. Each subject performed 6 repetitions of each time delay. Trials were repeated if the subject blinked frequently or signalled discomfort. Each trial started with an audible tone, with the spot at the centre of the screen, and was concluded after 15 s by a second audible tone. The complete experiment was repeated with and without the saccadic velocity threshold.

## Analysis

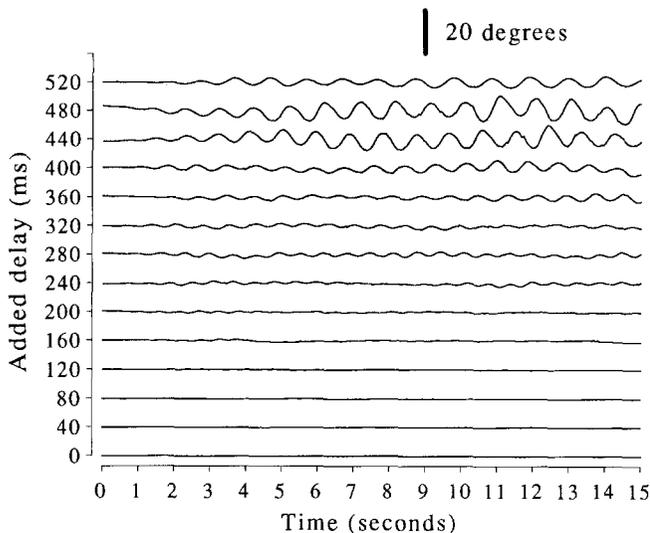
The period of oscillation of the eye about the target (limit cycles) was quantified. A Fourier transform was calculated for the eye position traces from each subject (15 s, 7500 points each). An average Fourier transform was then calculated from the six spectra per subject for each time delay. Oscillation period was taken as the location of the maximum power of the spectrum, excluding peaks at very low frequencies. A regression line was fitted to plots of oscillation period against imposed delay.

## Results

The effect of delaying visual feedback during fixation of a stationary target was to induce significant horizontal eye motion whose features depended on the added delay  $T_{\text{ext}}$ . A typical set of eye position traces with delays between 0 and 520 ms are shown in Fig. 2. The results of delaying both the smooth pursuit and saccadic eye movements were essentially similar – only data from the experiment in which smooth pursuit was selectively delayed are presented.

When delays of 20–160 ms were added the eye movements were indistinguishable from fixation of a stationary target with normal vision. The eye would be near-stationary at the start of the trial, but making normal micro-saccades and fine adjustments of position. These small eye movements were reflected in the target display, so the subjective impression was that the target "jittered" about a fixed point.

As the time delay reached a threshold of about 200 ms all subjects started to show sustained smooth oscillations: the target would begin to oscillate, reflecting the oscillations of the eye, as the subject unsuccessfully tried to match the movements of the target. At medium delays (e.g. 240 ms; Fig. 2), this oscillatory behaviour could wax and wane during the 15-s trials, but with the longer delays the



**Fig. 2.** Typical eye smooth pursuit position traces with different added delays. Each trace is the eye position signal plotted against time after removal of saccades and a quadratic trend (see Materials and methods), offset vertically to indicate the added delay. The calibration bar indicates the positional scale. For this subject (R.C.M.) limit cycles began at a delay of 160 ms

subjects typically entered sustained oscillations. As the delay was increased above the threshold of 200 ms the period of these limit cycles increased. The amplitude, in general, also increased with increasing delay, although the amplitude for any given delay would vary between trials. At the highest delays the target spot occasionally reached the limits of the oscilloscope screen and the displayed target motion under these conditions appeared discontinuous, as the target spot would remain stationary (but still visible) at one or other side of the screen until the delayed eye motion signal shifted it back onto the screen.

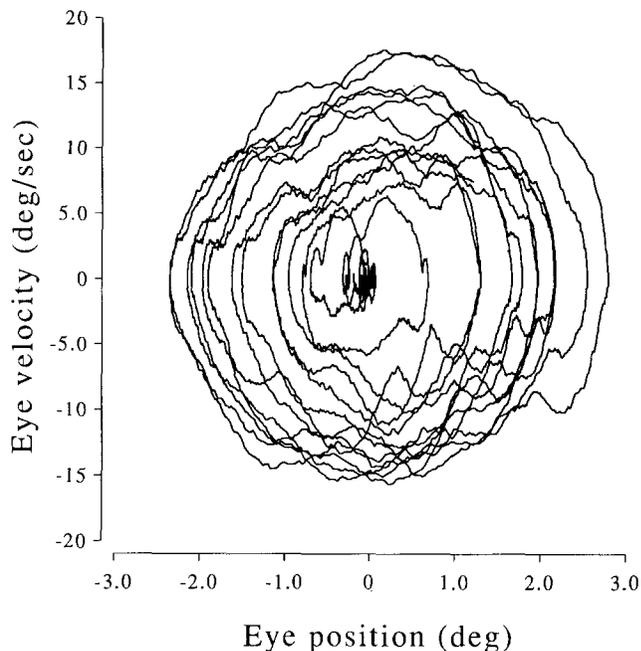
Over the 15 s of the trials the oscillations appeared to be stable and any growth in amplitude was slight. A phase plane plot of eye velocity against eye position is shown in Fig. 3 to demonstrate the route to the limit cycle through a spiral path.

#### Spectral analysis

The mean Fourier periodograms for each subject are shown in Fig. 4. Each spectrum has been plotted against the imposed delay, clipped at periods greater than 1500 ms (i.e. at frequencies below 0.66 Hz). Dots mark the location of the largest peak in the spectrum corresponding to the period of the limit cycle oscillations. The reasonably narrow peaks in the spectra demonstrate that the self-excited oscillations are roughly sinusoidal.

#### Dependence of oscillation period on $T_{ext}$

A significant correlation between added delay and oscillation period was found for all three subjects (Table 1;  $r^2 > 0.98$ ,  $P < 0.0001$ ). The period increased linearly with



**Fig. 3.** Phase plane plot of eye velocity against eye position for subject R.C.M. with an additional delay of 520 ms (see top trace, Fig. 2)

imposed delay, with a slope close to 1.5 and an intercept between 212 and 306 ms (Table 1; Fig. 7). When saccades were delayed as well as the smooth pursuit the slope was somewhat higher (1.6–2.0, intercept 233–311 ms); but the correlation between delay and oscillation period was still highly significant ( $r^2 > 0.89$ ,  $P < 0.0005$ ).

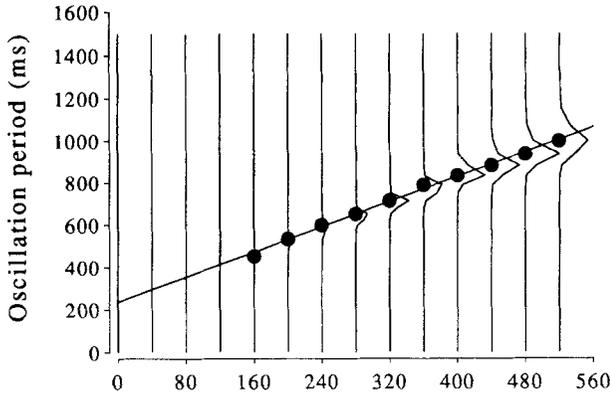
#### Model simulations

Simulations of the experimental paradigm were carried out using the Robinson (Robinson et al. 1986) and Lisberger (Krauzlis and Lisberger 1989) models. They were simulated on a digital computer using an iteration time step of 0.1 ms for 15 s. The experimental paradigm was simulated by adding in a single additional delay after the comparator for target and eye velocity (Fig. 1), thereby delaying retinal velocity error. To perturb the system a velocity pulse of  $5^\circ \text{ s}^{-1}$  was imposed onto an intrinsically stationary target for 50 ms. The subsequent behaviour was then observed and the period of any oscillations measured.

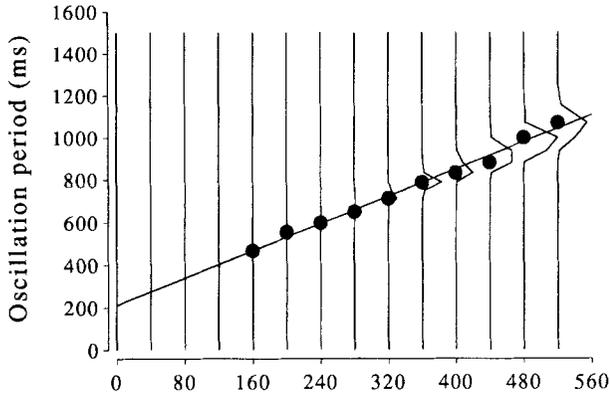
The Robinson model was positionally stable until 80 ms delay was added (Fig. 5). Between 80 and 240 ms additional delay the eye oscillated stably at 3.8 Hz with a small amplitude of about  $0.2^\circ$ . However, at delays above 240 ms the model broke down into slower oscillations which increased in amplitude. The increase in oscillation period with added delay was linear (Table 1) with a slope of 3.4 (Fig. 7).

The Lisberger model was stable with added delays up to 160 ms (Fig. 6). With larger delays the eye velocity very quickly reached saturation levels of  $90^\circ \text{ s}^{-1}$ . The increase in oscillation period with added delay was linear (Table 1)

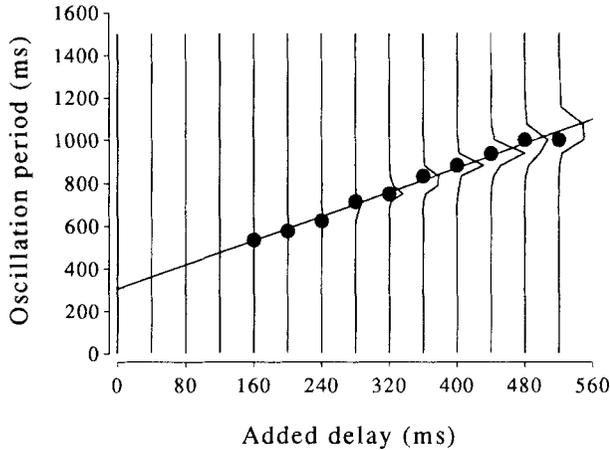
DMW



RCM



MAS



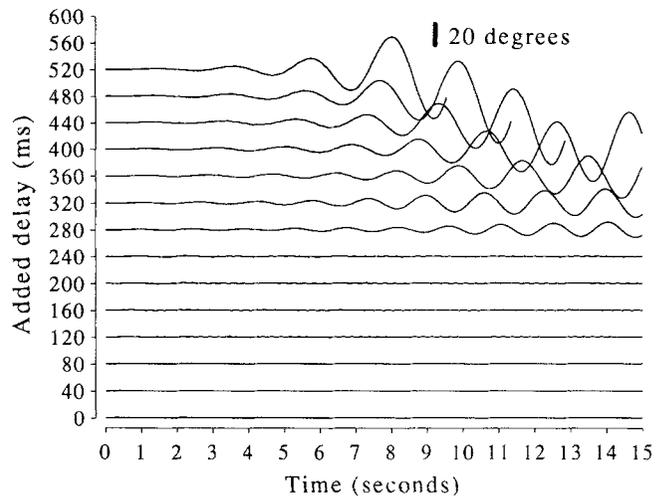
**Fig. 4.** Oscillation period of the limit cycles seen during fixation plotted against the added delay. The vertical traces are the averaged Fourier periodograms ( $n=6$ ) of the eye position records; the period of their peak is marked by the *dots*. A linear regression line has been fitted to the dots

and had a slope of 2.7 (Fig. 7). Neither model generated limit cycles at delays above 160 ms, but instead showed oscillations of increasing amplitude.

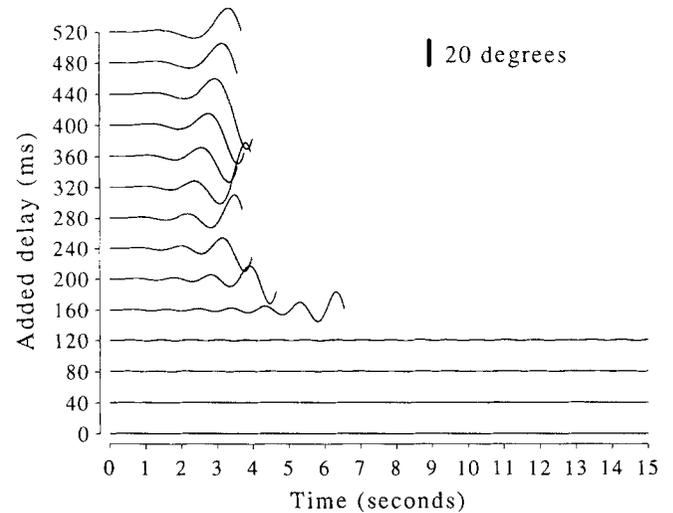
Finally we investigated differences in slope and intercept between the individual regressions shown in Table 1.  $t$  values for the pairwise comparisons between each possible combination of these five regressions are shown in Table 2. Asterisks indicate the significance levels of each result, which have been adjusted according to the Bonfer-

**Table 1.** Regression of limit-cycle period on imposed delay calculated from averaged periodograms from each subject, the combined experimental data and from the model simulations

Subject	$r^2$	$P$	Intercept (ms)		Slope	
			Mean	SE	Mean	SE
D.M.W.	0.99	<0.0001	237	11	1.48	0.03
R.C.M.	0.99	<0.0001	212	20	1.60	0.06
M.A.S.	0.98	<0.0001	306	20	1.41	0.06
Combined	0.98	<0.0001	252	16	1.50	0.04
Robinson	0.98	<0.0001	480	81	3.44	0.20
Lisberger	0.99	<0.0001	543	13	2.69	0.03



**Fig. 5.** Simulations of the Robinson model are shown in the same form as Fig. 2. Eye position traces with different added delays are shown. For clarity the records are clipped when eye velocity first exceeded  $90^\circ \text{ s}^{-1}$



**Fig. 6.** Simulations of the Lisberger model are shown in the same form as Fig. 2. Eye position traces with different added delays. For clarity the records are clipped in the cycle within which eye velocity first exceeded  $90^\circ \text{ s}^{-1}$

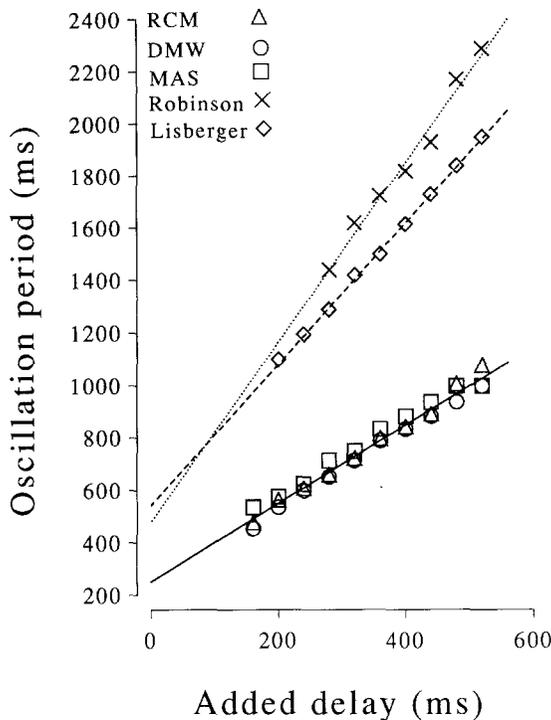


Fig. 7. Oscillation period against added delay with linear regression lines for subjects D.M.W., M.A.S. and R.C.M. and for simulations of the Robinson and Lisberger models. The three subject's data have been grouped to fit a single regression line (solid line)

Table 2. Pairwise comparison of regressions of oscillation period against added delay for the three subjects and two models

Regression	Intercept				
	D.M.W.	R.C.W.	M.A.S.	Robinson	Lisberger
D.M.W.		1.08	3.00	4.0*	18.51***
R.C.M.	1.91		3.31*	4.03*	13.27***
M.A.S.	1.09	2.43		2.61	9.61***
Robinson	13.0***	11.0***	12.14***		1.15
Lisberger	25.63***	15.29***	18.03***	4.75**	
	Slope				

*t* values below the diagonal are from the comparison of the slopes and *t* values above the diagonal are from the comparison of the intercepts

\* $P=0.05$ ; \*\* $P=0.01$ ; \*\*\* $P=0.001$

roni technique. Table 2 shows that the Robinson and Lisberger models had significantly different slopes, although the intercepts were not significantly different. There were no significant differences between the slopes of any pair of subjects; the intercept for one pair was significantly different at the 5% level. The regression slopes for all three subjects were significantly different ( $P < 0.001$ ) from the slope of the Robinson model and two of the subjects had an intercept significantly different at the 5% level. The regression slopes and intercepts for all three subjects were significantly different ( $P < 0.001$ ) from those of the Lisberger model.

## Discussion

In this paper we report the short-term sensitivity of the oculomotor system to imposed delays. Above a delay threshold of about 160 ms the eye fell into limit-cycle oscillations. The period of the oscillations was linearly related to the imposed feedback delay, with a slope close to 1.5 and a mean intercept of 252 ms, which is about twice the intrinsic delay of 125 ms measured by pursuit latencies (Robinson 1965). Recent evidence suggests that fixation and pursuit movements are controlled separately (Luebke and Robinson 1988; Goldreich et al. 1992). Although the task employed here is initially one of fixation, the imposed feedback delay effectively shifts the eye into pursuit for much of the time. The significant results discussed below relate only to these oscillatory responses, and are not derived from, nor apparently influenced by, the preceding fixation response. We therefore discuss these data in relation to the control of pursuit eye movements.

Independently, Goldreich et al. (1992) have performed a similar experiment in monkeys in which they introduced added feedback delays during a ramp pursuit task and recorded eye oscillation in the ensuing 2–3 s. As they increased the added delay the eye oscillation period increased and when plotted their results were mostly bounded by lines with slopes of 2 and 4. From their published results, the slopes measured in the three monkeys were greater than 2.

The results presented above are significantly different from the simulations of both the Robinson and Lisberger pursuit models. The combined results are shown in Fig. 7, in which a single regression line has been fitted to the data from all three subjects, for comparison with the simulations. Neither the existence of limit cycles nor the relationship of the period of oscillation to added delay can be explained by the two models. We will now focus on what can be deduced from these data, about the form of controller.

Many physiological systems are regulated by negative feedback control, characterised at their simplest by a gain and a delay. If either the gain or time delay is too high the feedback system becomes unstable and will tend to oscillate. For a linear system such oscillations grow indefinitely. In practice such oscillations are limited by nonlinearities present in the system, and usually steady limit cycles ensue.

Several authors have observed self-excited, low-frequency, smooth oscillations of the eye under artificial feedback paradigms in which the feedback gain is altered (Doesschate 1954; Riggs and Tulunay 1959; Fender and Nye 1969; Steinbach and Pearce 1972; Scotto and Oliva 1984). For example Scotto and Oliva (1984) reported limit cycles when the open loop gain was modified from its normal value of  $-1$ . Although there were intersubject differences in the oscillation period ranging between 900 and 1820 ms, there was little intra-subject variability as the gain was changed. They concluded that nonlinearities must be present in the oculomotor system, as they are critical to the maintenance of the limit cycles.

There have also been studies of the effects of delayed feedback on smooth pursuit eye movements. One of the

earliest was by Smith et al. (1970) who examined sinusoidal tracking and showed that as the delay was increased tracking became increasingly saccadic. They showed that the frequency and magnitude of the saccades increased with increasing delays. We confirmed this observation in our experiment in which both smooth pursuit and saccades were delayed. More recently, Goldreich and Lisberger (1987) have shown that in monkeys the ringing frequency seen in response to a ramp target depends on the feedback delay, and they concluded that such ringing is visually driven. Deno et al. (1989) also demonstrated oscillations during ramp tracking when a delay of 80 ms was imposed. They showed that the monkey could partially adapt to the delay, so that after several days the oscillations shifted towards a higher frequency. In this study we have also demonstrated that the oculomotor system can be pushed into oscillations by changing just the smooth pursuit feedback time delay, and that the system settles into quite stable limit cycles.

Limit cycles, which are independent of external excitation, are a nonlinear phenomenon. Others have also suggested that there are nonlinearities in the smooth pursuit system. For example, Saint-Cyr and Fender (1969) showed that it fails to obey the superposition principle in the frequency domain (a necessary condition for a linear system). Thus there seems little doubt that the control system is nonlinear. Studies have also demonstrated particular nonlinearities, such as velocity saturation at  $50\text{--}70^\circ\text{ s}^{-1}$  (Westheimer 1954; Rashbass 1961; Robinson 1965; Young 1971) and saturation of the peak acceleration and the amplitude of ringing, as the target ramp velocity is increased (Lisberger et al. 1981; Robinson et al. 1986). The fact that neither the Robinson or Lisberger models showed limit cycles with delayed feedback implies that their nonlinearities are not sufficiently powerful.

The other feature of the oculomotor controller is the consistent relationship between oscillation period and imposed delay. A linear feedback system will spontaneously oscillate at the frequency at which the open-loop phase lag is  $180^\circ$ . The phase lags in a linear system can be split into those which are due to pure time delays and those due to lags in the other components such as the plant and controller. Consider a linear system with a phase lag of  $\theta$  degrees due to the controller and plant, but excluding both the intrinsic time delays in the system ( $T_{\text{int}}$ ) and the added time delay ( $T_{\text{ext}}$ ). The oscillation period  $p$  corresponds to the frequency at which the phase shift due to  $\theta$  and the two time delays combine to equal  $180^\circ$ :

$$\theta + \frac{360 T_{\text{int}}}{p} + \frac{360 T_{\text{ext}}}{p} = 180$$

therefore

$$p = \frac{360(T_{\text{ext}} + T_{\text{int}})}{180 - \theta}$$

So the period,  $p$ , is related to added delay,  $T_{\text{ext}}$ , with a slope of  $360/(180 - \theta)$  and intercept of  $360 T_{\text{int}}/(180 - \theta)$ . These relationships may not be so straightforward in nonlinear systems; Mackey and Glass (1977) report that a

nonlinear feedback system can display oscillations with periods of 2–4 times the intrinsic delay, dependent on both its nonlinearities and phase lags. The linear relationship between oscillation period and added delay reported here is therefore not surprising. However, the finding that the slope was about 1.5 and the intercept twice the intrinsic delay suggests that  $\theta$ , the intrinsic open loop lag of the system, is small and may be negative.

The major difference between our results from the experiments with and without a saccadic threshold was the difference in regression slope, which rose from around 1.5 to 2.0 when saccades were included. This may be a sign of entrainment between the two nonlinear control loops. The intercepts did not differ significantly.

The Lisberger model has two main features which contribute to the phase lag (Fig. 1b). The first is the velocity pathway which together with the integrator contributes approximately  $90^\circ$  of phase lag. The second is the acceleration pathways which contain both a differentiator (to derive accelerations from velocities) which develops a phase advance, and an integrator which causes a phase lag. These effects combine to produce a phase lag close to zero for the acceleration pathways. The combined contribution of the parallel velocity and acceleration paths generates a phase lag between  $0$  and  $90^\circ$ . The precise value of the lag depends on the relative gains of the pathways. Although Goldreich et al. (1992) point out that their model can have lags between  $0$  and  $90^\circ$  (and thereby slopes between 2 and 4) depending on their model's parameters, a total lag of zero is only possible if the gain of the velocity pathway is zero. This controller would then act solely on acceleration and therefore could not be a valid model of smooth pursuit.

The Robinson model also contains non-zero controller lags due to its integrator; it has an effective phase lag of around  $90^\circ$  at a frequency of about 1 Hz. Thus both the Robinson and Lisberger models have phase lags greater than zero; hence they exhibit a slope of oscillation period against added delay higher than 2.0. So the behaviour seen in our experiment was certainly unexpected. A zero or negative phase lag suggests that there must be effective compensation for the plant's dynamics. This could be achieved either through predictive control (Barnes and Asselman 1992), by which the results of the motor command are predicted and can therefore be used before they would be available by feedback alone. Alternatively an inverse model of the plant (Jordan and Rumelhart 1992) could be employed to cancel out the phase lags of the eye.

In summary, the results cannot be explained by either the Robinson or Lisberger models. Firstly, limit cycles seen are not produced by either of the two models, suggesting that they do not capture the nonlinear behaviour of pursuit or that their nonlinearities are not sufficiently strong. Secondly, our observation of a slope of 1.5 and intercept of about twice the intrinsic delay suggest that the models fail to match the phase lags of the oculomotor system. If the smooth pursuit controller takes account of the dynamic components that Robinson and Lisberger propose, then there must also be compensation to reduce the overall phase lag, either by prediction or by the use of inverse models.

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