

## ON THE PREDICTIVE CONTROL OF FOVEAL EYE TRACKING AND SLOW PHASES OF OPTOKINETIC AND VESTIBULAR NYSTAGMUS

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### SUMMARY

1. Smooth pursuit and saccadic components of foveal visual tracking as well as more involuntary ocular movements of optokinetic (o.k.n.) and vestibular nystagmus slow phase components were investigated in man, with particular attention given to their possible input-adaptive or predictive behaviour.

2. Each component in question was isolated from the eye movement records through a computer-aided procedure. The frequency response method was used with sinusoidal (predictable) and pseudo-random (unpredictable) stimuli.

3. When the target motion was pseudo-random, the frequency response of pursuit eye movements revealed a large phase lead (up to about 90°) at low stimulus frequencies. It is possible to interpret this result as a predictive effect, even though the stimulation was pseudo-random and thus 'unpredictable'.

4. The pseudo-random-input frequency response intrinsic to the saccadic system was estimated in an indirect way from the pursuit and composite (pursuit + saccade) frequency response data. The result was fitted well by a servo-mechanism model, which has a simple anticipatory mechanism to compensate for the inherent neuromuscular saccadic delay by utilizing the retinal slip velocity signal.

5. The o.k.n. slow phase also exhibited a predictive effect with sinusoidal inputs; however, pseudo-random stimuli did not produce such phase lead as found in the pursuit case.

6. The vestibular nystagmus slow phase showed no noticeable sign of prediction in the frequency range examined (0 ~ 0.7 Hz), in contrast to the results of the visually driven eye movements (i.e. saccade, pursuit and o.k.n. slow phase) at comparable stimulus frequencies.

### INTRODUCTION

In many instances, the human oculomotor system is capable of changing its response characteristics depending upon the stimulus predictability. This is evident when the eye tracks a moving visual target using saccadic and pursuit movements;

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frequency response experiments have shown that the phase lag at a given frequency is significantly smaller when the target motion is sinusoidal than when random (Stark, Vossius & Young, 1962; Young & Stark, 1963; Dallos & Jones, 1963). In fact, values of the phase lag with sinusoidal stimuli are substantially smaller than those expected from the neuromuscular delay. It is generally believed that the effect is a manifestation of underlying c.n.s. predictive mechanisms; presumably, the stimulus wave form is analysed and its periodicity is detected and utilized to compensate for the inherent neuromuscular delay, which results in improved accuracy of visual fixation. The nature of ocular responses shortly after a sudden onset or cessation of periodic inputs is consistent with such an interpretation (Dallos & Jones, 1963; Vossius, 1965). The prediction hypothesis is supported further by the finding of Kowler & Steinman (1979*a*) that smooth pursuit movements were produced in advance of expected step or ramp changes of a visual target.

Similar predictive phenomena have been demonstrated, with the frequency response method, in the vergence system for binocular fixation (Zuber, 1965) as well as in the accommodation control mechanism of the ocular lens (Stark, Takahashi & Zames, 1965). An analogous predictive effect is known in manual control (McRuer & Krendel, 1959; Stark, Iida & Willis, 1961). Prediction was not, however, found in the human pupillary system (Stark, 1968). As regards animal experiments, the eye tracking systems of the monkey (Lisberger & Fuchs, 1978; Lisberger, Evinger, Johanson & Fuchs, 1981) and the cat (Evinger & Fuchs, 1978) appear to have predictive ability. There is also neurophysiological evidence in the monkey that some cells in the abducens nucleus start to increase their discharge rate before the predictable visual trigger to make a saccadic movement (Mohler & Wurtz, 1976), and also that some Purkinje cells in the cerebellum show a predictive firing pattern in response to sinusoidal target motion (Lisberger & Fuchs, 1978; Suzuki, Noda & Kase, 1981).

In this paper, we describe some new results concerning the predictive oculomotor function in man. Although both saccadic and pursuit movements are used for tracking a continuously moving target, earlier results were concerned with the predictive characteristics of the composite (saccade + pursuit) system as a whole. The relative contribution of each subsystem to the predictive effect has not been clarified in spite of ample physiological and clinical evidence indicating that saccadic and pursuit movements are served by separate c.n.s. controls. The first experiment reported investigates this problem. In a second experiment, the optokinetic nystagmus (o.k.n.) was also studied to examine whether its slow phase component shows a predictive input-adaptation. As opposed to foveal tracking with saccadic and pursuit movements, o.k.n. comprises eye movements of a more involuntary nature evoked by homogeneous motion of a large visual field rather than a small visual object. In the third experiment, the slow phase component of vestibular nystagmus was similarly examined. This ocular reflex is a non-visual one, yet phylogenetically related to o.k.n.

## METHODS

Throughout the present series of experiments, the data were frequency responses measured with sinusoidal and pseudo-random inputs. Four subjects were used. Binocular vision was allowed, but only the horizontal movement of the right eye was measured using a pulsed infra-red photo-electric device (Model SGHV-2; Biometrics Inc.). This limbus tracking instrument was adjusted to operate in a linear range of  $\pm 15^\circ$  in the horizontal direction with accuracy of about  $0.25^\circ$ . A computer was used to identify and separate the slow and quick eye movement components, both of which were present in each class of horizontal eye movement investigated. Appropriate precautions were taken to control the stimulus magnitude to minimize non-linear characteristics of the oculomotor system and/or instruments as described in the following methodological details which depended on the type of eye movement.

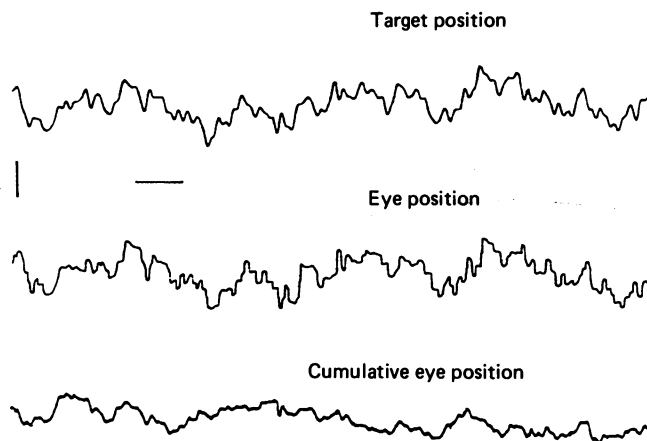


Fig. 1. Sample traces showing the data processing of foveal tracking records by the MITNYS program. From top to bottom, target position, eye position and cumulative eye position. Saccades were removed from the eye position record and the smooth portion connected to obtain the cumulative eye position. Calibrations  $10^\circ$  and 5 s.

*Pursuit component*

A moving target spot was generated on a Hewlett-Packard 1300 X-Y cathode ray tube and projected through a convex lens onto a white screen confronting the subject. The cathode ray tube was set for its maximum intensity. The curvature of the screen was adjusted so that the target angular position seen by the subject was proportional to the linear displacement on the cathode ray tube. The driving signal for pseudo-random target motion was the sum of sixteen sinusoids of harmonically unrelated frequencies (Young & Stark, 1963). Its band width was controlled by changing the frequency composition. A set of four pseudo-random test signals was obtained in this way: A, 0.04–2.80 Hz; B, 0.04–1.40 Hz; C, 0.03–0.70 Hz and D, 0.45–2.30 Hz. During each sinusoidal or pseudo-random stimulation the target velocity was kept below  $20^\circ/\text{s}$  and was thus well under the pursuit saturation level. A hybrid computer program, MITNYS (Allum, Tole & Weiss, 1975), was applied to piece together pursuit movements by removing saccadic jumps. The result was a continuous curve referred to as 'cumulative eye position'. A sample trace is shown in Fig. 1. Frequency responses of the pursuit system were then computed by applying a 1024-point fast Fourier transform (f.f.t.) program to the input-output data set of target position and cumulative eye position. Only those frequency components that were contained in the input were considered in the analysis. Higher order harmonics were often present in the response spectrum but were generally not significant. Frequency responses of the composite (saccadic + pursuit) system were also measured. In this case, the f.f.t. program was applied directly on the stimulus-response records.

### Saccadic component

Normally, an adequate stimulus to the saccadic system needs to undergo discrete changes of its position. To measure a random-input frequency response of the saccadic system, one might use as a target motion steps of random duration and amplitude. However, an alternative method was employed here which required no such additional experiments, but made use of the preceding composite and pursuit random-input frequency response data.

Let  $y_c$ ,  $y_s$  and  $y_p$  represent the angular positions of the eye due to composite, saccadic and pursuit (cumulative) movements, respectively. It follows then that at time  $t$

$$y_s(t) = y_c(t) - y_p(t).$$

Saccadic movements act to eliminate fixation position errors left uncorrected by the pursuit system; were the pursuit tracking perfect, there would be no saccadic movements in response to a continuous target motion, except for a possible initial adjustment. Hence, the stimulus that the saccadic system sees is

$$x_{\text{eff}}(t) = x(t) - y_p(t), \quad (1)$$

where  $x(t)$  is the target position relative to the subject, and  $x_{\text{eff}}(t)$  is the effective input to the saccadic system. Thus, the composite system of Fig. 2A can be decomposed into the pursuit and saccadic

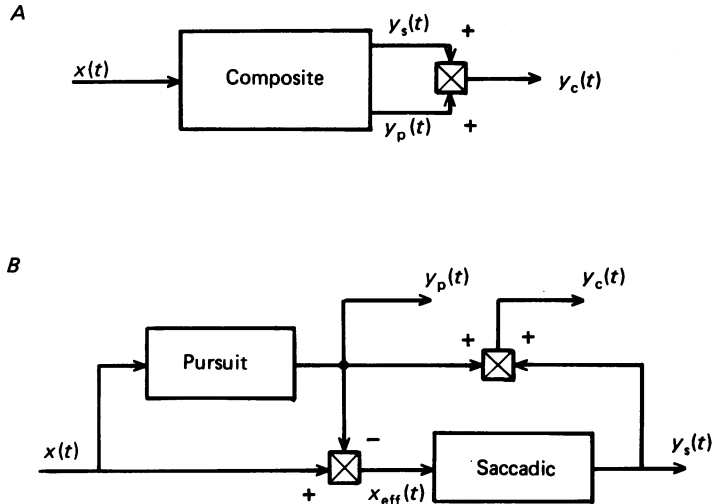


Fig. 2. A diagram showing two equivalent representations, *A* and *B*, of the foveal tracking system. In *B*, the pursuit and saccadic systems are separated. See text for the significance of symbols.

subsystems as illustrated in Fig. 2*B*. In the analysis to follow, we invoke an approximation that the oculomotor system is deterministic, time-invariant, and linear. By  $G_c(j\omega)$ ,  $G_p(j\omega)$  and  $G_s(j\omega)$ , we denote the transfer functions of the composite, pursuit and saccadic systems, respectively. Here  $\omega = 2\pi f$  is the angular frequency,  $f$  the frequency in Hz, and  $j = \sqrt{-1}$ . It follows then that

$$G_s(j\omega) = y_s(j\omega)/x_{\text{eff}}(j\omega), \quad (2)$$

$$\begin{aligned} y_s(j\omega) &= y_c(j\omega) - y_p(j\omega) \\ &= (G_c(j\omega) - G_p(j\omega)) x(j\omega), \end{aligned} \quad (3)$$

and using eqn. (1),

$$\begin{aligned} x_{\text{eff}}(j\omega) &= x(j\omega) - y_p(j\omega) \\ &= (1 - G_p(j\omega)) x(j\omega). \end{aligned} \quad (4)$$

From eqns. (2)–(4), one finds

$$G_s(j\omega) = \frac{G_c(j\omega) - G_p(j\omega)}{1 - G_p(j\omega)}. \quad (5)$$

In view of eqn. (2),  $G_s(j\omega)$  is an *intrinsic* saccadic frequency response, as opposed to an *apparent* saccadic frequency response given by

$$y_s(j\omega)/x(j\omega) = G_c(j\omega) - G_p(j\omega). \quad (6)$$

Compare eqns. (5) and (6), and note the difference factor of  $1 - G_p(j\omega)$ . The intrinsic frequency response emphasizes that it is  $x_{\text{eff}}(t)$  (the target position minus the pursuit correction) rather than  $x(t)$  which actually drives the saccadic system. Thus, the random-input intrinsic frequency response was measured indirectly by using eqn. (5) together with experimental data points (median values) of  $G_c(j\omega)$  and  $G_p(j\omega)$ .

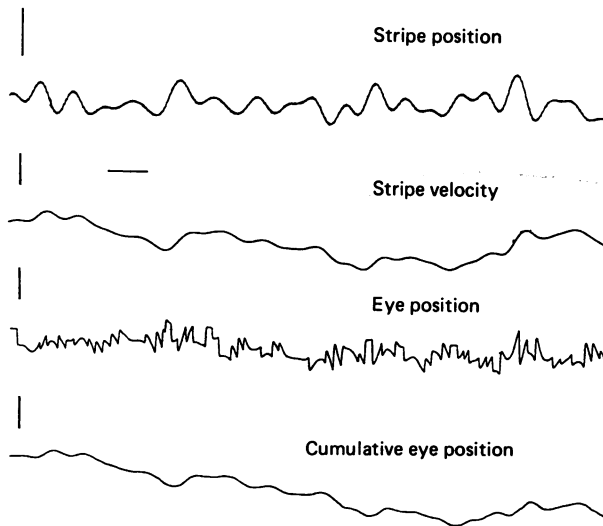


Fig. 3. Sample traces showing the data processing of o.k.n. records by the MITNYS program. From top to bottom, position of a representative stripe, field velocity of the stripe pattern, eye position and cumulative eye position. Corresponding calibration bars are  $45^\circ$ ,  $40^\circ/\text{s}$ ,  $10^\circ$  and  $45^\circ$ , respectively. Time calibration 2 s.

#### *O.k.n. slow phase*

The experimental apparatus was the same as that described in the preceding foveal tracking experiment. Horizontally moving vertical stripes to elicit o.k.n. were generated on the cathode ray tube by means of a computer graphical technique (Yasui, Tole & Young, 1977). The stimulus pattern covered  $\pm 45^\circ$  of the subject's visual field in the horizontal plane, and  $34^\circ$  up and  $15^\circ$  down in the vertical plane. Stripe separation was  $6^\circ$  and stripe width  $0.6^\circ$ . The subject was instructed to stare at the pattern, rather than to pursue individual stripes. Some practice was needed to avoid conscious fixation or pursuit. Signals A, B, C, D described earlier were employed again to drive the pseudo-random inputs. The field velocity of the stripe pattern was kept well below the saturating value of o.k.n. slow phase, which was about  $35^\circ/\text{s}$ . The MITNYS-f.f.t. data processing was applied in a manner analogous to the foveal tracking experiment; the MITNYS program removed each fast phase movement in order to obtain the cumulative eye position representing the slow phase component. A sample trace is shown in Fig. 3. The f.f.t. routine was then applied to evaluate the frequency responses to sinusoidal and pseudo-random motions of the stripe pattern.

*Vestibular nystagmus slow phase*

The subjects with eyes open were oscillated about the vertical axis in the dark. This was done using a rotating chair apparatus described elsewhere (Yasui & Young, 1975). The chair motion was recorded through a helical potentiometer. To provide brisk nystagmus, alertness was maintained through a mental arithmetic task. During the sinusoidal stimulation, the chair oscillation frequency was varied in a random order ranging from 0.025 to 0.70 Hz. Peak angular velocity of the chair never exceeded  $40^\circ/\text{s}$ . The pseudo-random vestibular stimulation was provided with a sum of ten harmonically unrelated sinusoids from 0.03 to 0.70 Hz. The peak velocity of each sinusoid was kept below  $15^\circ/\text{s}$ . By means of the MITNYS-f.f.t. processing, the data were analysed in exactly the same manner as in the foregoing o.k.n. case.

## RESULTS

*Composite (pursuit + saccade)*

The frequency responses of the composite (pursuit and saccade) system are shown in Fig. 4. Open circles are median data points with the sinusoidal stimulation, and filled circles the pseudo-random stimulation with stimulus A (see Methods). Since data were collected based on one determination per subject at each stimulus frequency, the standard deviations indicate differences among the four subjects used. (This comment applies to all the relevant figures in this paper.)

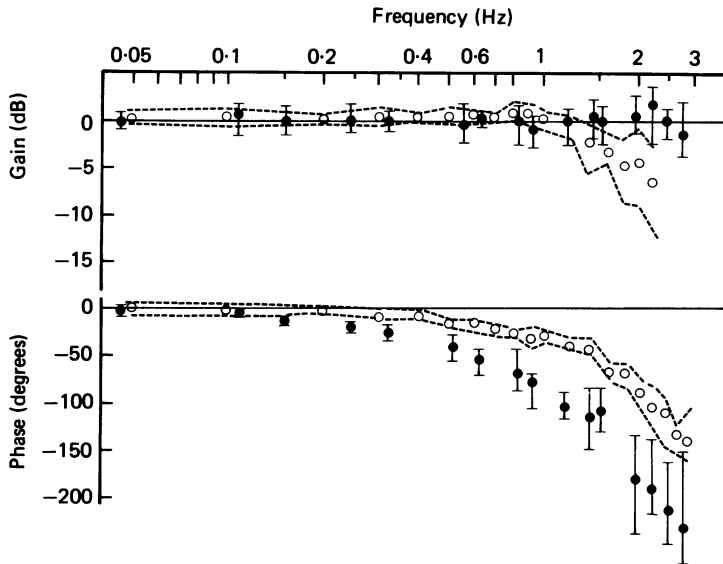


Fig. 4. The frequency responses of the composite (pursuit + saccade) tracking system. Sinusoidal (○) and pseudo-random (●) stimulations. Median values with  $\pm$  s.d. range (bars and dashed segments). Four subjects.

The phase lag was reduced significantly in the sinusoidal case compared to the pseudo-random case, as has been reported by many authors (Stark, Vossius & Young, 1962; Young & Stark, 1963; Dallos & Jones, 1963; Michael & Melvill Jones, 1966; Werner, Wunder & Jahns, 1972). Frequency responses were also obtained with our other pseudo-random stimuli (B, C and D), each having a different band width. Such results (not shown) confirmed Michael & Melvill Jones' (1966) observation that the phase lag at a given frequency increased as the stimulus band width increased; in other words, as the target motion became more difficult to anticipate.

*Pursuit component*

With sinusoidal inputs, the smooth pursuit system yielded virtually the same phase response (not shown) as in the composite case. The gain deterioration at higher frequencies, however, was more pronounced than in the composite case. This is in accord with the consideration that saccadic movements occur more often at higher frequencies due to the increasing need to back up the pursuit tracking (Young & Stark, 1963).

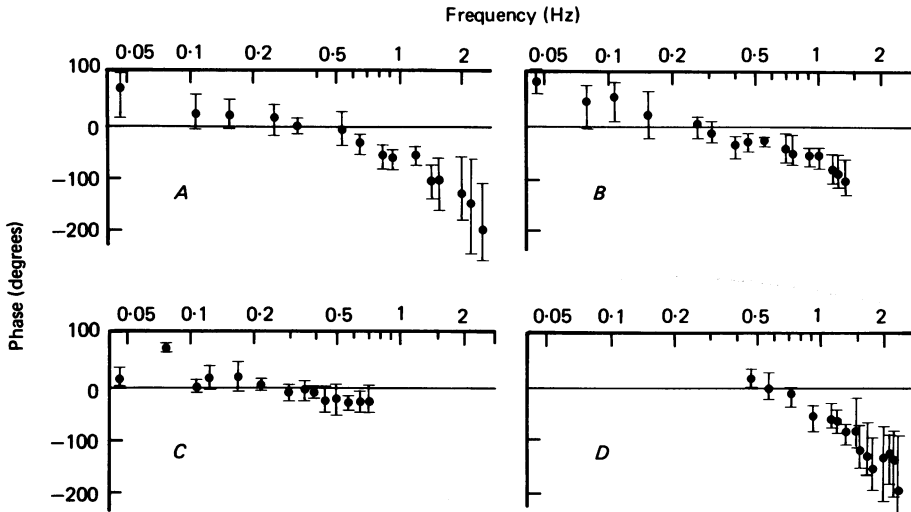


Fig. 5. Phase shifts in the frequency responses of the pursuit system to the pseudo-random inputs. A, B, C and D show results for test signals A, B, C and D respectively as defined in Methods. Median values with  $\pm$  s.d. range. Four subjects.

When the input was pseudo-random, the pursuit system suffered from gain drop over the entire frequency band of each of the four pseudo-random stimuli we tested. This indicates the importance of saccadic corrections even at low frequencies when the target motion was pseudo-random. The phase result is given in Fig. 5. It shows a conspicuous trend of large phase lead at lower frequencies within each stimulus band. With stimulus B, for example, the median value of the phase lead reached as much as  $84^\circ$  at 0.046 Hz. At increasing frequencies, the phase lead became less and the response eventually lagged behind the stimulus. For each stimulus band, there was some intermediate frequency giving no phase shift. This rather peculiar result was not likely due to an experimental or computational artifact, because the o.k.n. slow phase (shown later) never produced such a low frequency phase lead even though the analysis method was identical using MITNYS and f.f.t. with the same set of pseudo-random input signals. Thus, the result suggests some kind of input-adaptation of the pursuit system. This will be discussed later.

*Saccadic component*

Fig. 6 shows the apparent ( $\circ$ ) and intrinsic ( $\bullet$ ) saccadic frequency responses, which were computed from the composite and pursuit frequency response data according to the procedure given in the Methods. The target motion stimulating the

composite system was driven by the pseudo-random stimulus B. The two results differ considerably from each other. For comparison, Dallos & Jones' saccadic phase result (1963) with periodic square-wave target motion is reproduced in Fig. 6 (triangles). The phase shift was much reduced in this case and even some negative latency was present around 0.5 Hz, indicating a strong predictive effect. The present intrinsic frequency response will be discussed later in the light of a quantitative analysis.

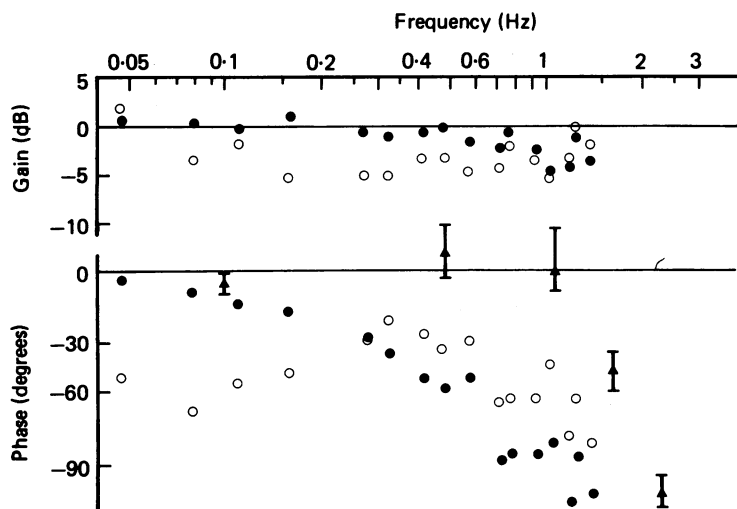


Fig. 6. The apparent (○) and intrinsic (●) frequency response of the saccadic system subjected to pseudo-random stimulation, as obtained from the composite and pursuit frequency response data according to the calculation in the Methods. The phase result with periodic square-wave target motion (triangles) is from Dallos & Jones. (1963).

#### *O.k.n. slow phase*

Fig. 7 shows the frequency responses of the optokinetic nystagmus slow phase with sinusoidal stimulation (○) and with pseudo-random stimulus A (●). The sinusoidal case is in general agreement with Gresty & Halmagyi's measurement (1979). In comparison, the pseudo-random case shows a greater increase of the phase lag with the stimulus frequency. This difference indicates a predictive input-adaptation of the o.k.n. slow phase system.

If the o.k.n. slow phase and pursuit systems are compared for their frequency responses to sinusoidal stimulation, then little difference ( $P < 0.05$ ) can be found in either gain or phase. (Compare open-circle data points of Figs. 4 and 7.) The pseudo-random stimulation, however, made a clear difference; unlike the result of Fig. 5 for foveal pursuit tracking, no phase lead is seen for the o.k.n. slow phase. Thus, the underlying input-adaptive mechanisms probably differ between the pursuit and o.k.n. slow phase systems.



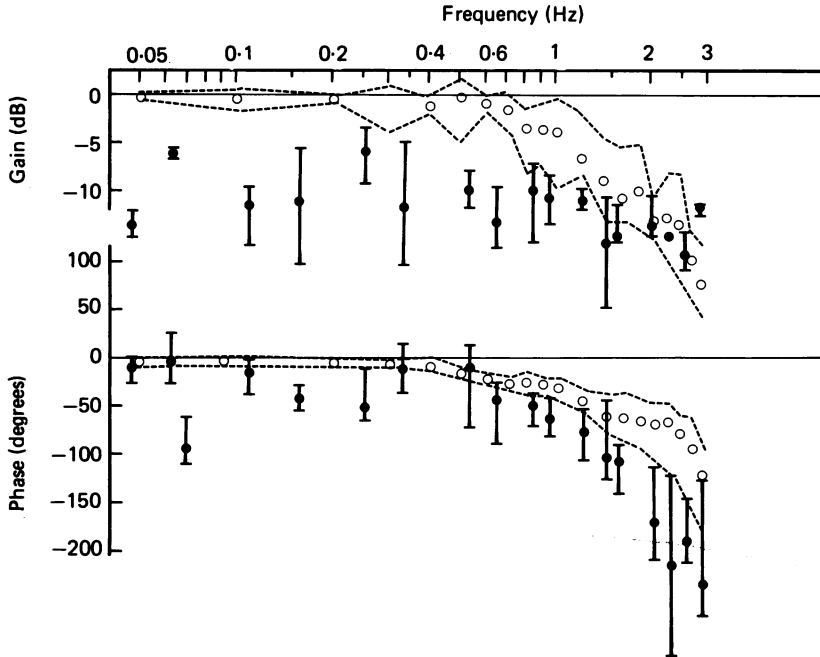


Fig. 7. The frequency response of the optokinetic nystagmus slow phase with sinusoidal (○) and pseudo-random (●) stimulations. Median values with  $\pm$  s.d. range (bars and dashed segments). Four subjects.

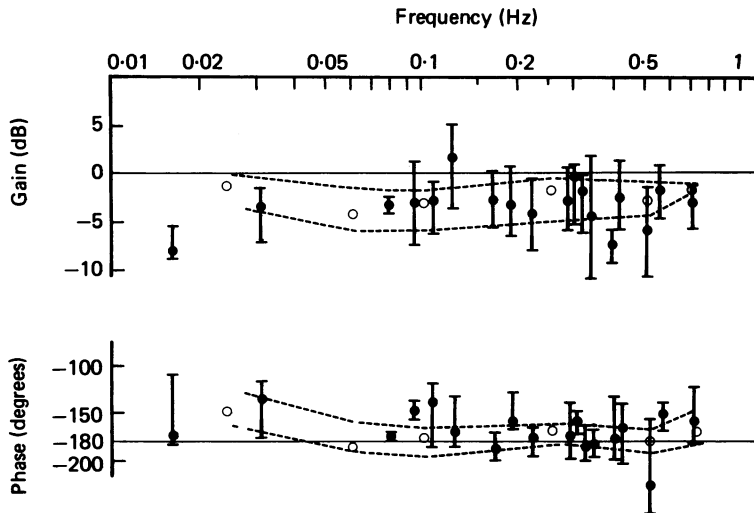


Fig. 8. The frequency response of the vestibular nystagmus slow phase with sinusoidal (○) and pseudo-random (●) stimulations. Median values with  $\pm$  s.d. range (bars and dashed segments). Four subjects.

*Vestibular nystagmus slow phase*

Fig. 8 shows the frequency response characteristics of the vestibular nystagmus slow phase. The input was the rotating chair position while the output was the cumulative eye position. A perfect eye stabilization against head rotation would require the gain to be 1 (or 0 dB) and the phase shift  $-180^\circ$ . The present situation deviated somewhat from this as expected from the dynamics of the semicircular canal at the lower stimulus frequencies as used here. Our results for the sinusoidal case (○) agree well with the results of others (e.g. Benson, 1969) under similar conditions (i.e. sinusoidal head oscillation in humans).

When the sinusoidal (○) and pseudo-random (●) cases of Fig. 8 are compared, no statistically significant difference can be found ( $P < 0.05$ ). Thus, prediction is not involved in the vestibulo-ocular reflex, at least over the frequency range tested in this experiment.

## DISCUSSION

*On the input-adaptation of the pursuit system*

The latency of human pursuit movements is about 150 ms, a value measured with ramp target motions consisting of a series of random (unpredictable) changes in velocity and direction (Westheimer, 1954; Rashbass, 1961). The latency of 150 ms would then predict a phase lag of at least  $54^\circ$  at 1 Hz and  $107^\circ$  at 2 Hz. However, when the input was sinusoidal, the phase lag gave smaller values;  $28^\circ$  at 1 Hz and  $88^\circ$  at 2 Hz. Thus, this difference can be accounted for by a compensatory predictive mechanism.

The input-adaptation of the pursuit system is characterized further by large phase leads at low stimulus frequencies in response to pseudo-random inputs (Fig. 5). This result is not straightforward to interpret. For instance, consider the phase lead of  $84^\circ$  obtained at 0.046 Hz. It might mean that the pursuit prediction was as much as 5.1 s ahead in anticipating the 0.046 Hz component of the pseudo-random stimulus. This would be quite improbable, however. Instead, it appears that the pursuit tracking was optimized to minimize its average phase shift at some mean frequency within the stimulus band, at the expense of low frequency over-compensation, resulting in the excess phase lead. This would also account for the observation that the phase lead became more conspicuous with increasing input band width and disappeared with sinusoidal test stimuli. According to this interpretation, the pursuit system has a predictive mechanism of its own that operates even when the target motion is pseudo-random or 'unpredictable'. This notion parallels that of Kowler & Steinman (1979*b*) who have discovered pursuit drifts preceding saccadic responses to unpredictable changes of target position. It is relevant to cite a preview-type manual control experiment (Drewell, 1972) in which the joy-stick movement showed a similar low frequency phase lead when the target motion was pseudo-random.

One may wonder what neural information the pursuit predictive mechanism operates upon. The retinal image information is the first signal received by the C.N.S. and represents the error signal (difference between target and eye motions) as commonly treated in servo models. This signal, however, is hardly very useful for

prediction, because we know that it is normally maintained small and therefore less predictable. A suggestion can be made based on the 'perceptual feedback hypothesis' (Yasui & Young, 1975; Barr, Schultheis & Robinson, 1976; Young, 1977; Lisberger *et al.* 1981), for which some neurophysiological evidence is available (Miles & Fuller, 1975; Lisberger & Fuchs, 1978). Thus, the perceived visual input motion, reconstructed in the c.n.s. by adding the oculomotor efferent copy (corollary discharge) to the retinal slip velocity signal, might be the signal processed by the predictive pursuit mechanism.

*Comparing pursuit, o.k.n. and vestibular nystagmus in the predictive input-adaptation*

The sinusoidal input frequency response was not much different between the pursuit and o.k.n. slow phase systems, showing a similar predictive effect apparently compensating for the oculomotor delay. This is in contrast with the absence of prediction in the o.k.n. slow phase in the rabbit which, however, lacks foveal eye tracking (Collewijn, 1969). However, when the stimulation was made pseudo-random in our experiment, a significant difference emerged between the two systems as evidenced by the large low frequency phase lead only seen in the pursuit case. The similarity in the sinusoidal case makes it unlikely that the difference in the pseudo-random case might be due to some interference of o.k.n. fast phase jumps with slow phase movements and hence might not necessarily represent an intrinsic distinction between the pursuit and o.k.n. slow phase system characteristics.

It is not entirely clear whether o.k.n. and pursuit movements are governed by separate subsystems of the visual and oculomotor system or by a single system operating differently in response to various types of stimuli (Henn, Cohen & Young, 1980). Although the present result does not necessarily resolve this problem, we can at least suggest that the two types of eye movement are endowed with different levels of input-adaptive capability. As reviewed by Robinson (1975), there is some evidence indicating that the visual cortex is necessary for the normal pursuit tracking but not for the o.k.n. In this light, coupled with other information (Lisberger & Fuchs, 1978; Pellionisz & Llinas, 1979; Suzuki *et al.* 1981), the phase-lag-reducing compensatory effect found in both systems with sinusoidal inputs is most likely to occur in the cerebellum, and the large phase lead found only in the pursuit response with pseudo-random inputs probably originates in the cerebral cortex, thus enabling a higher level of prediction.

With regard to the vestibular nystagmus, it has been shown in the conscious cat that the fast phases do not interfere with the slow phase movements (Donaghy, 1980); unlike the situation in the ether-anaesthetized cat (Sugie & Melvill Jones, 1971). This assures the validity of the present separation analysis procedure to estimate the frequency responses of the slow phase system. Our data indicating the absence of prediction in this oculomotor reflex were very much limited as regards the testing frequency range (0.02–0.7 Hz), in comparison with animal experiments reported in the literature (e.g. Fernández & Goldberg, 1971; Donaghy, 1980). Predictive effects were, however, clearly evident at similarly low frequencies in all the visually induced eye movements (i.e. pursuit, saccade and o.k.n. slow phase) that we have investigated in this research.

Vestibular nystagmus and o.k.n. have probably evolved together for the same

behavioural end, i.e. a stabilization of retinal images which otherwise would be smeared during head movements. Interaction between these two oculomotor reflexes can be seen at behavioural as well as neurophysiological levels (Henn, Young & Finley, 1974; Robinson, 1975; Koenig, Allum & Dichgans, 1978; Henn, Cohen & Young, 1980). However, the o.k.n. slow phase has a predictive function but the vestibular nystagmus slow phase probably does not. Perhaps, therefore, visual inputs are necessary for the underlying predictive mechanisms to function.

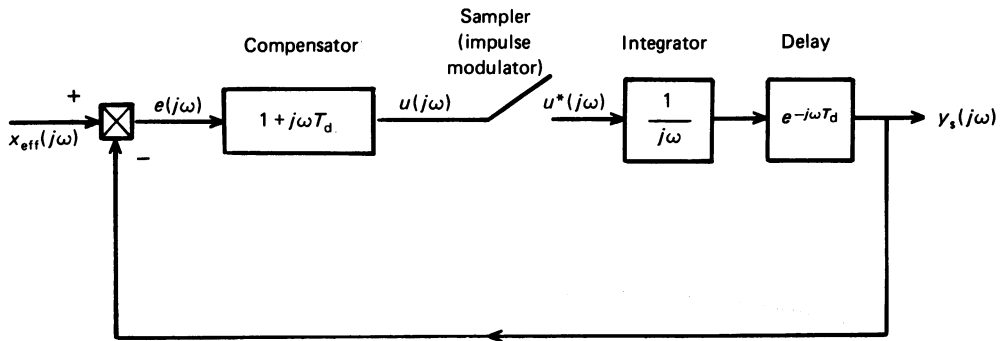


Fig. 9. The sampled data feed-back control model for the saccadic system used to discuss the intrinsic frequency responses result of Fig. 6.

*The intrinsic saccadic frequency response, and a servo model with predictive compensation*

We have estimated the frequency response intrinsic to the saccadic system driven by pseudo-random stimulation. This result (Fig. 6) is accounted for well by a control-theoretic analysis. Fig. 9 shows our model, which is a modification of the sampled-data servo model of Young & Stark (1963) for the saccadic system subjected to unpredictable inputs. In Fig. 9, let  $T_m$  be the sampling interval which corresponds to the mean time interval between two successive saccades.  $T_m = 510$  ms was estimated as an average over the four subjects with stimulus B in the experiment of Fig. 6. Another parameter  $T_d$  appears twice in the model; as  $e^{-j\omega T_d}$  and as  $1 + j\omega T_d$ , where  $j = \sqrt{-1}$  and  $\omega = 2\pi f$  with  $f$  being the frequency in Hz. The factor  $e^{-j\omega T_d}$  represents a pure delay with delay time  $T_d$ , and in the model it accounts for the saccadic latency. Thus,  $T_d = 200$  ms is assumed (e.g. Westheimer, 1954). The element  $1 + j\omega T_d$  is a phase-advancing network, and it compensates for the saccadic latency. Evidence for this is discussed shortly.

Comparison between experiment and theory is presented at this point. As shown by the analysis given in the Appendix, the model predicts (through eqn. (A 5)) the intrinsic saccadic frequency response as shown in Fig. 10. The prediction is good up to about 0.6 Hz, beyond which it deteriorates as expected from the sampled-data theory (see the Appendix).

The network  $1 + j\omega T_d$  in the model accounts for Rashbass' (1961) experiment of a constant velocity target motion preceded by an initial displacement in the opposite direction. When the stimulus was of this type, the subject would follow the target with a single pursuit movement, failing to produce a saccade despite a large initial

deviation of the retinal image. This occurred most often when the step size and the ramp velocity were such that the target re-crossed its starting position after 150–200 ms, approximately the saccadic delay time  $T_d$ . Thus, it appears that the size of a fixation saccade is not simply based on the position error at the sample time, but rather is based on the position 150–200 ms ahead, as anticipated by taking into account the retinal error rate. This suggests that an operator of the form  $1 + T_d d/dt$  (or equivalently  $1 + j\omega T_d$  in the frequency domain) acts upon the retinal position error signal (Robinson, 1968). This is a simple and approximate way to offset the saccadic

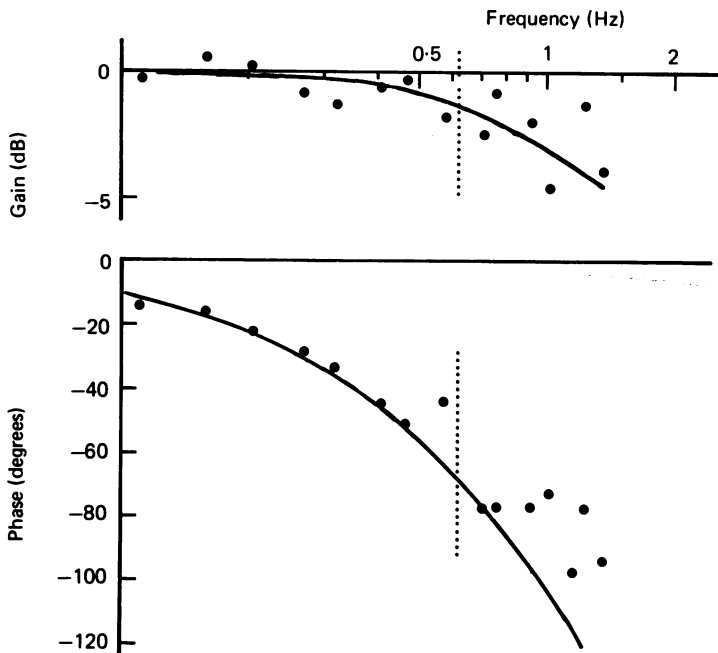


Fig. 10. A control theoretic prediction (continuous curves) of the intrinsic saccadic frequency response based on the sampled-data servo model of Fig. 9. The model is valid up to 0.62 Hz, as indicated by the dotted line. Experimental data (●) replotted from Fig. 6.

delay  $T_d$ , as incorporated in the present model. Dallos & Jones (1963) have demonstrated that the human saccadic system has an excellent capability to tune itself to periodic stimuli (Fig. 6, triangles). Sugie (1968) presented a model to account for such a resonance-like phenomenon. The compensatory effect in the Rashbass (1961) step ramp experiment, on the other hand, appears to be of a more primitive type that has also been observed in the cat (Evinger & Fuchs, 1978). If it can be called predictive, then one wonders whether this type of prediction may occur not only with step ramp targets but also with more general unpredictable inputs to the saccadic system. The model analysis result of Fig. 10 implies this to be indeed the case. The present model includes a 'predictive' compensatory network to account for the saccadic response to 'unpredictable' inputs, but it is not intended to explain the frequency tuning (Fig. 6, ▲) that Dallos & Jones (1963) have shown with periodic ('predictable') stimuli. The type of prediction shown in this model is merely

extrapolation based on derivatives rather than temporal pattern synchronization. As we have seen, the saccadic frequency response to the pseudo-random ('unpredictable') input (Fig. 6, ●), which is reconciled well with our servo model (Fig. 10), indicates the saccadic tracking to be still much less accurate than in the periodic case (Fig. 6, ▲). It follows that a prediction more potent than one considered here is at work when the saccadic input is periodic.

## APPENDIX

The sample data model for the saccadic system (Fig. 9) can be analysed as follows. If  $e(j\omega)$  denotes the target position relative to the retina, then

$$e(j\omega) = x(j\omega) - y_c(j\omega) = x(j\omega) - y_p(j\omega) - y_s(j\omega).$$

But,

$$x(j\omega) - y_p(j\omega) = x_{\text{eff}}(j\omega)$$

from eqn. (1), and hence

$$e(j\omega) = x_{\text{eff}}(j\omega) - y_s(j\omega).$$

As shown in Fig. 9, this is passed through a phase-lead compensator whose output  $u(j\omega)$  is the signal to be sampled by an impulse modulator. The saccadic response then is

$$y_s(j\omega) = \frac{e^{-j\omega T_d}}{j\omega} u^*(j\omega). \quad (\text{A } 1)$$

Here, the symbol \* indicates the impulse modulation due to sampling (e.g. Jury, 1958). Thus,

$$u^*(j\omega) = \frac{1}{T_m} \sum_{n=-\infty}^{\infty} u(j\omega + jn\omega_0) \quad (\text{A } 2)$$

where  $T_m$  is the sampling interval and  $\omega_0 = 2\pi f_0 = 2\pi/T_m$  is the angular frequency of sampling. The actual sampling interval, which manifested itself as the time duration between successive saccades, was not constant but fluctuated. In this analysis, however, the system is approximated as deterministic and  $T_m$  corresponds to the mean value of sampling intervals.

Input B used to drive the pseudo-random target motion had its highest frequency component at 1.34 Hz.  $T_m = 510$  ms was estimated by taking the mean value over four subjects. Hence, the sampling frequency of the model is set at  $f_0 = \omega_0/2\pi = 1.96$  Hz. The Nyquist frequency was  $f_0/2 = 0.98$  Hz, not high enough to cover the stimulus band width of 1.34 Hz. As a result, any two successive summation terms in eqn. (A 2) overlap each other somewhat. With this in mind, it follows from eqn. (A 2) and the foregoing numerical consideration that

$$u^*(j\omega) = \frac{1}{T_m} u(j\omega - 2n\pi j \times 1.96),$$

$$f = \frac{\omega}{2\pi} = 1.96 n \sim 1.96 n + 0.62 \text{ Hz,}$$

$$u^*(j\omega) = \frac{1}{T_m} [u(j\omega - 2n\pi j \times 1.96) + u(2(n+1)\pi j \times 1.96 - j\omega)],$$

$$f = 1.96 n + 0.62 \sim 1.96 n + 1.34 \text{ Hz},$$

$$u^*(j\omega) = \frac{1}{T_m} u(2(n+1)\pi j \times 1.96 - j\omega),$$

$$f = 1.96 n + 1.34 \sim 1.96 (n+1) \text{ Hz}.$$

Here,  $n = 0, +1, \dots$ , and  $0.62 \text{ Hz} = 1.96 \text{ Hz} - 1.34 \text{ Hz}$ . Thus, if one considers only the non-overlapping frequency region of the lowest degree ( $n = 0$ ), then

$$u^*(j\omega) = \frac{1}{T_m} u(j\omega), \quad f = \frac{\omega}{2\pi} = 0 \sim 0.62 \text{ Hz}. \quad (\text{A } 3)$$

$u(j\omega)$  is expressible as

$$\begin{aligned} u(j\omega) &= (1 + j\omega T_d) e(j\omega) \\ &= (1 + j\omega T_d) x_{\text{eff}}(j\omega) - y_s(j\omega) - j\omega T_d y_s(j\omega). \end{aligned}$$

The last term is equivalent to  $-T_d dy_s(t)/dt$ . It represents an impulse train since  $y_s(t)$  is saccadic steps. However, this impulse train signal is practically lost in the sampling process because of the loop time delay  $T_d$  coupled with the statistical and asynchronous nature of the sampling. One may therefore write

$$u(j\omega) = (1 + j\omega T_d) x_{\text{eff}}(j\omega) - y_s(j\omega). \quad (\text{A } 4)$$

From eqns. (A 1), (A 3), (A 4), we finally obtain

$$G_s(j\omega) = \frac{y_s(j\omega)}{x_{\text{eff}}(j\omega)} = e^{-j\omega T_d} \frac{1 + j\omega T_d}{e^{-j\omega T_d} + j\omega T_m}, \quad (\text{A } 5)$$

which is valid for  $f = \omega/2\pi = 0 \sim 0.62 \text{ Hz}$ . This is the (pseudo-random input) intrinsic saccadic frequency response of the model, which is shown in Fig. 10.

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