

EYE MOVEMENT DYNAMICS IN THE DOGFISH

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SUMMARY

A method is described of obtaining the relationship between electrical stimulation of the abducens nerve and horizontal eye movement in the dogfish. The stump of the VIth nerve was stimulated intracranially in a fish in which the brain had been removed, but in which the circulation remained intact, and the gills were perfused with sea water. Horizontal rotation of the eye was monitored with an opto-electronic movement detector. Eye rotation was linearly related to stimulus frequency in the 0–20 Hz range, and was maximal at frequencies above 40 Hz. Stimulation of the VIth nerve, with a pulse train whose frequency was modulated sinusoidally between 0 and 20 Hz, produced sinusoidal eye movements. The frequency response of the system approximates a first order low pass filter with a characteristic frequency of 0.23 Hz, and an additional phase lag equivalent to a time delay of approximately 50 ms.

INTRODUCTION

The control of eye movement is one of the most studied, and best understood, vertebrate motor control systems. The system is amenable to study for several reasons: for example, the functions of eye movements are known, detailed mechanical analysis can be made, and eye movements can be induced through several reflex pathways.

Eye movement mechanics have been extensively studied in mammals (e.g. Collins, 1977) in which despite the complexity of the movements, a single first order model provides a satisfactory description of the system for most purposes (Carpenter, 1977; Robinson, 1981). The parameters of the model can be obtained from a knowledge of the eye mechanics (Robinson, 1965), the relationship between motoneurone firing and eye movement (Robinson, 1981) or the movement responses to nerve stimulation (Zuber, 1968*a*). The last of these methods is perhaps the easiest to carry out and provides a characteristic frequency (2.5 Hz) which is in good agreement with Robinson's mechanical model (Carpenter, 1977). Eye movement responses to nerve stimulation are probably dominated by the faster motor units, and represent an overestimate of the characteristic frequency of the transfer function relating eye movement to motoneuronal firing. The characteristic frequency obtained from the behaviour of an average motoneurone is around 0.7 Hz (Robinson, 1981). The practice of representing

a complex physiological system as a single first order model must be treated with caution, but for the case of the oculomotor system this approach is justified in that it provides a simple description which is commensurate with observed behaviour.

Due to the accessibility of the labyrinth the physiology of the elasmobranch vestibular system is well known (e.g. Lowenstein, 1974; O'Leary, Dunn & Honrubia, 1976), and indeed these studies have been fundamental to our understanding of the sensory transduction process. Aspects of the central vestibular pathways have been investigated (Montgomery & Roberts, 1979; Montgomery, 1982) and their responses to horizontal head rotation determined (Montgomery, 1980). The operation of the horizontal vestibulo-ocular reflex during swimming in dogfish has been studied by Harris (1965). Two components of the direct horizontal vestibulo-ocular pathway thus remain to be characterized: the transfer characteristics from vestibular to oculomotor neurones, and the transfer characteristics of the oculomotor system itself. This study provides a characterization of the oculomotor system.

MATERIALS AND METHODS

Experiments were performed on the carpet shark *Cephaloscyllium isabella* caught in trawl nets, or on long-lines, and kept in seawater circulation at the Leigh Marine Laboratory. In fish anaesthetized with Tricaine (by immersion in a 0.02% solution in sea water), the cranium was opened and the brain removed leaving the stumps of the cranial nerves accessible intracranially. Bleeding was controlled by cautery and fish were then placed in a tank and the gills perfused with sea water at the ambient temperature of 14°C. The stump of the abducens nerve (cranial nerve VI) was secured in a suction electrode, and the cranial cavity filled with elasmobranch Ringer.

Electrical stimuli were trains of supramaximal square wave pulses (0.5 ms, 1.5–2 V). Pulse trains were delivered at a constant frequency in the range 0–50 Hz, or sinusoidally modulated between 0–20 Hz at modulation frequencies in the range 0.01–1 Hz (Fig. 1).

Eye movements produced by electrical stimulation of the VIth nerve were recorded by an opto-electronic movement detector (Helvesen & Elsner, 1977). A small patch (4 mm²) of 'Scotchlite' brand reflective sheeting was fixed to the eye by cyano-acrylate glue. The reflective patch was illuminated through a semireflective mirror (Fig. 1). The patch reflected light back along the incident path, through the semireflective mirror and onto a photodetector (PIN-SC, United Detextor Technology, Santa Monica, Cal. U.S.A.) built into the film plane of a camera. The voltage output of the photodetector was directly related to the position of the eye patch, and was calibrated at the conclusion of each experiment. The linear movement of the patch was converted into an angular measure by simple trigonometry on the assumption that the eye rotated about its centre. Eye movements were monitored on a storage oscilloscope and chart recorder.

RESULTS

The preparation exhibited little or no deterioration in its response to a standard pulse train over periods as long as 2–3 days.

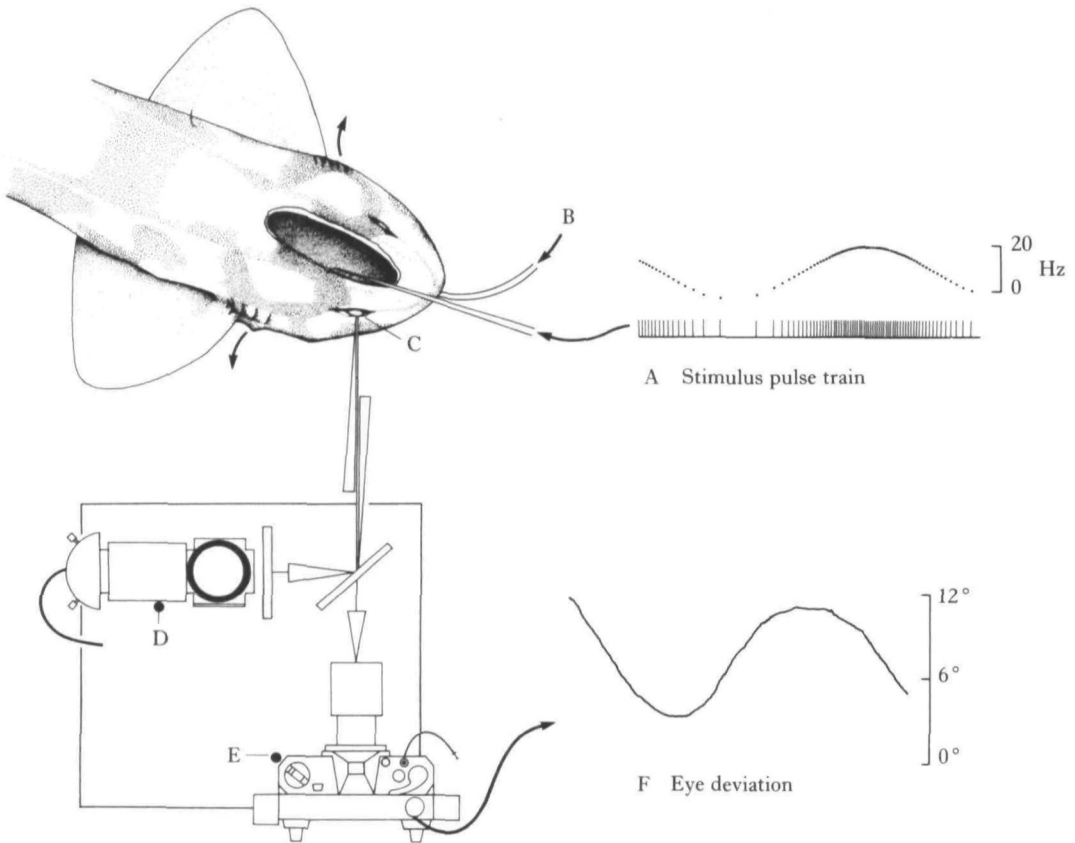


Fig. 1. The carpet shark preparation. (A) Sinusoidally modulated, or constant frequency, pulse trains are applied to the Vth nerve *via* a suction electrode. (B) Sea water is passed over the gills of a fish in which the brain has been removed. A retro-reflective patch is attached to the eye (C) and illuminated (D) *via* a half silvered mirror (arrows represent the light path). Eye rotation is monitored by an opto-electronic movement detector mounted in the film plane of the camera (E). (F) Example of eye movement record.

The frequency response curve for the preparation (Fig. 2) was determined by presenting a 10 s pulse train at each frequency. This length of pulse train was sufficient to obtain a plateau response at all frequencies; at 20 Hz the plateau was reached after 3–5 s. The relationship between eye position and stimulus frequency was approximately linear up to about 20 Hz, but saturated at frequencies above this. The maximum eye rotation of about 15° was obtained by stimulus frequencies of 35 Hz and above.

The latency of the response measured from the oscilloscope was approximately 50 ms, comprising conduction, synaptic and excitation-contraction coupling delay.

Sinusoidally modulated pulse trains (0–20 Hz) produced sinusoidal eye movement (Fig. 3). At low modulating frequencies (0.01 Hz) the gain for each fish was arbitrarily assigned the value of 1. The Bode plot, or log gain *versus* log modulation frequency, is shown in Fig. 4A. The solid line represents the best fit first order model of the form:

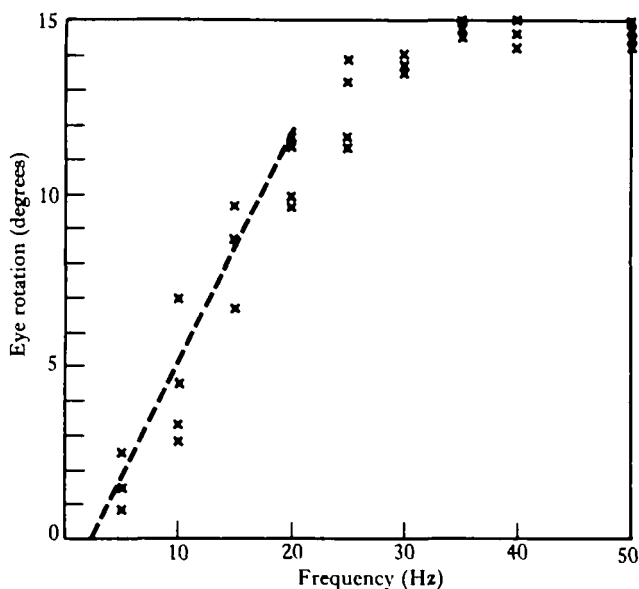


Fig. 2. Frequency response curve. Maximum eye deviation induced by 10 s, constant frequency pulse trains in the range 0–50 Hz. The response is linear in the 0–20 Hz range and saturates at higher frequencies.

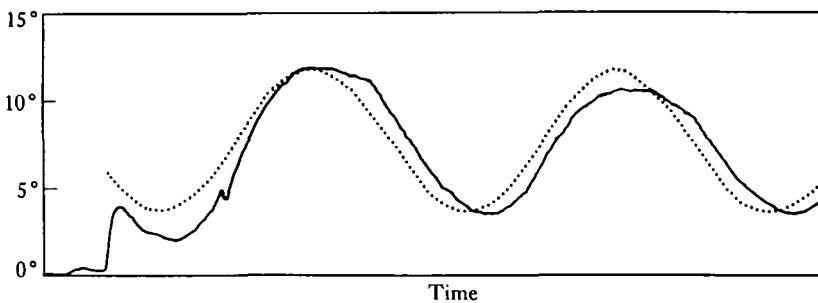


Fig. 3. Record of eye movement response to sinusoidally modulated pulse train. Solid line is a record of eye movement in degrees, dotted line represents stimulus wave form (peak-to-peak 0–20 Hz, modulation frequency 0.05 Hz). Note the phase lag of the response at this low modulation frequency.

$$G(f) = \frac{1}{\sqrt{1 + (f/f_c)^2}}$$

where: G is gain; f_c is characteristic frequency and f is modulation frequency determined by a non-linear regression technique (Helwig & Council, 1979). The characteristic frequency is 0.23 Hz (95 % confidence interval is between 0.21 and 0.26 Hz).

The Bode plot for the phase difference between stimulus and response waveform peaks is shown in Fig. 4B. The upper solid line represents the theoretical first order model. The lower solid line takes account of the phase contribution of the time delay. There is a systematic deviation of phase from that predicted from the model at low modulation frequencies. This low frequency phase lag is also apparent in the original record illustrated in Fig. 3.

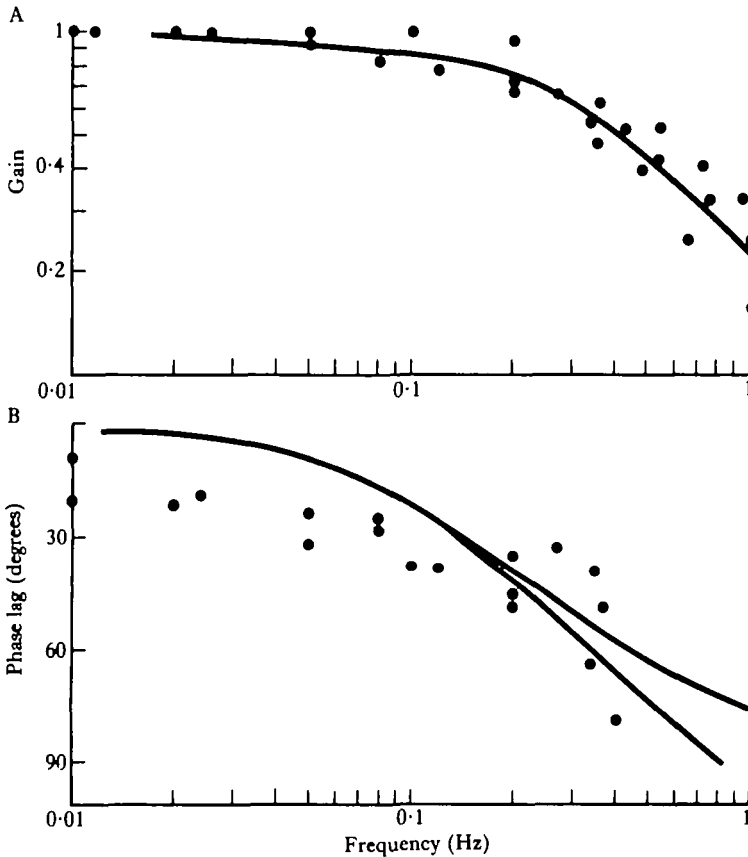


Fig. 4. Bode plots of gain and phase vs modulation frequency (see text for details). (A) Log gain vs log modulation frequency. Three fish were used, dots represent the means of 10 measurements of gain from one fish at a particular modulation frequency, the solid line represents the best fit first order model. (B) Phase lag vs log modulation frequency. The upper solid line represents the theoretical first order model, the lower line takes account of the phase contribution of the time delay. Each point represents the mean of 10 phase measurements for one fish. Note the low frequency phase lag.

DISCUSSION

The linear region of the stimulus response curve (between 0 and 20 Hz) probably corresponds to the natural operating region of the oculomotor system (Zuber, 1968*b*). This implies that the operating frequencies of oculomotor neurones in the carpet shark are considerably lower than those reported for other animals. In mammals oculomotor firing rates are amongst the highest known, up to 800 Hz in some primates (Fuchs & Luschei, 1970). In other fish, firing rates are also comparatively high, around 300–400 Hz in goldfish (Hermann, 1971; Gestrin & Sterling, 1977). The lower firing rate in *Cephaloscyllium* is correlated with the observation that carpet sharks have a poorly developed saccadic system. There is virtually no spontaneous eye movement when they are lying quiescent in the tanks, and like other dogfish studied (Harris, 1965) the eye movements during swimming are primarily compensatory, the only eye movements of any speed occurring just before the fish turns. For this reason it is difficult to obtain estimates of saccade velocity, but the saccades occurring during

nystagmus induced by vestibular (horizontal canal) stimulation are in the range 10–15°/s (unpublished observation). It is also likely that the low operating range of the oculomotor system reported here is in part due to the lower temperature at which these recordings were made. There is evidence in other preparations that a reduction in temperature produces a parallel lowering of the frequency response curve (Truong, Wall & Walker, 1964; Fisher & Florey, 1981; MacDonald & Montgomery, 1982).

Stimulation with sinusoidally modulated pulse trains provides a useful description of the oculomotor system. The relationship between gain and modulation frequency is similar to that of a first order low pass filter which can be specified by its characteristic frequency. It is notable that the characteristic frequency is nearly one order of magnitude less than that found for the cat oculomotor system (Zuber, 1968a).

The same model provides a reasonable prediction of the phase relationship between stimulus and response (at higher stimulus frequencies than those shown in Fig. 4 allowance would have to be made for the additional phase lag contributed by the time delays in the system). Systematic departure from the model is shown at low modulation frequencies. This is possibly due to the activation of the slow fibres which occur in the extraocular muscle in carpet shark (unpublished observation). The slow response of this component of the muscle is equivalent to a degree of integration in the response which would introduce phase lag at low frequency.

The natural frequency of head movement in these fish is in the range 0.1–1 Hz. Harris (1965) shows an example of a fish swimming at 0.4 Hz with eye position in phase with head position. At this frequency maximum firing in the vestibular primary afferents would be in phase with head velocity (Montgomery, 1980), that is 90° phase advanced with respect to head position. The present study shows that at this same frequency there is considerable phase lag between motoneurone firing and eye position (Fig. 4B). For this reason the velocity signal of the contralateral canal and secondary vestibular cells will be appropriate to drive the abducens motoneurons directly; there is less requirement for an integration step in this pathway as is postulated in higher vertebrates (Carpenter, 1977). The paucity of saccadic eye movements, and correspondingly low characteristic frequency, may enable the vestibulo-ocular reflex system in carpet shark to operate satisfactorily without substantial central processing of the sensory signal.

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