

OPTOKINETIC RESPONSES, VISUAL ADAPTATION AND MULTISENSORY CONTROL OF EYE MOVEMENTS IN THE SPINY LOBSTER, *PALINURUS* *VULGARIS*

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SUMMARY

1. The optokinetic responses of the spiny lobster, *Palinurus vulgaris*, were measured in the vertical roll plane. The eyes followed the stripes without nystagmus, and demonstrated incomplete bilateral coupling. Closed-loop responses to oscillating stripes (20° peak-to-peak) showed marked habituation at frequencies above 0.1 Hz, but at lower frequencies continued undiminished, with amplitude-gain values approaching 1.0.

2. Changes in illuminance level demonstrated that the optokinetic response exhibited a threshold below which the eye initially failed to detect and follow the stripes. However, over a period of several minutes, the previous response level could be restored or even exceeded.

3. The optokinetic response could be antagonized by a response to the irradiance gradient, which also had a threshold and showed adaptation. Migration of visual screening pigments may underlie these adaptation processes.

4. Optokinetic stimuli could interact with proprioceptive inputs arising from displacements of the legs on a moving platform. When the proprioceptive inputs were of equal frequency and in antiphase, the optokinetic response was reduced in amplitude; it was in phase with the visual stimulus at low frequencies, and in phase with the platform in the high-frequency range. When the inputs had unequal frequencies, the eyes followed the drum if its frequency was low, but failed to follow either drum or platform if drum frequency was high. We conclude that multisensory control extends the frequency range of operation of compensatory eye movements, and is dominated by the low-frequency optokinetic response.

INTRODUCTION

Compensatory eye movements and equilibrium reactions in decapod crustaceans are performed with reference to three spatial parameters: gravity, substrate orientation and visual field (Schöne, 1980; Neil, 1982). These responses contribute in different

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ways and to different extents to the overall reaction in the species so far investigated (*Procambarus clarkii*: Wiersma & Oberjat, 1968; Hisada, Sugawara & Higuchi 1969; Fay, 1973; Olivo & Jazak, 1980; *Panulirus interruptus*: York, Yanagisawa & Wiersma, 1972; *Carcinus maenas*: Horridge, 1966; Wiersma & Fiore, 1971), but little is known about the interrelationships of the responses. This paper forms one of a series to investigate the mechanism of multisensory interaction in the spiny lobster, *Palinurus vulgaris*.

The contribution of mechanosensory inputs from statocysts and from leg proprioceptors to compensatory eye movements in *Palinurus* has been studied in some detail, with particular reference to responses in the roll plane (Schöne, Neil, Stein & Carlstead, 1976; Schöne, Neil & Scapini, 1978; Schöne & Neil, 1977; Neil & Schöne, 1979; Birkner, 1978; Scapini, Neil & Schöne, 1978; Neil, Schöne & Scapini, 1979). Studies in other decapods, particularly on the optokinetic system, suggest a major role for vision in the control of eyestalk position (Horridge & Sandeman, 1964; Wiersma & Oberjat, 1968; York *et al.* 1972). The response characteristics of the visual system in *Palinurus* are described in this paper, and we also consider how visual inputs interact with proprioceptive inputs from the legs. An analysis of the combined control system, which involves in addition the response to gravity, is presented elsewhere (Schöne, Neil, Scapini & Dreissman, 1983).

MATERIALS AND METHODS

Spiny lobsters (*Palinurus vulgaris* Latreille = *Palinurus elephas* Fabricius) from the Mediterranean were kept under semi-natural conditions in tanks of recirculated sea water. General procedures for preparing and mounting the animals are described elsewhere (Schöne *et al.* 1976). Optokinetic stimulation was provided by a half-cylinder of translucent Plexiglass, radius 14.5 cm and length 21 cm, upon which 11 black stripes 2 cm wide were mounted 2 cm apart. This drum was mounted over the animal with the axis of the frame coincident with that of the platform, and the stripes parallel to the animal's longitudinal axis (Fig. 1). With the lobster in position, the angle subtended at the eye by a stripe period was approximately 30°. Additional panels carrying a pattern of radiating stripes were inserted in front of the animal. The drum was illuminated either by two 60 W (J s^{-1}) lamps at 5–10 cm distance (Fig. 1), or by one such light source 20 cm above. The irradiance measured inside the drum at the level of the eye was 1200 lx with the former arrangement and 50 lx with the latter. For experiments with varying irradiance, neutral density filters (Kodak Wratten) were placed in the light path from the single overhead source. In some experiments, a translucent drum without stripes was used, in conjunction with translucent panels in front of the animal. Both drums produced a bright upper field of illumination. The platform itself, being made of translucent material, significantly reduced the visibility of stationary edges in the animal's ventral field of view.

Movements of the drum assembly and the platform were produced by eccentric drives from d.c. motors which could be driven over a wide range of speeds by the appropriate choice of gearbox and voltage. These stimuli were monitored using precision potentiometers. Movements of the left eye were measured using a miniature angle transducing device (Marrelli & Hsiao, 1976). The transducer wire could be

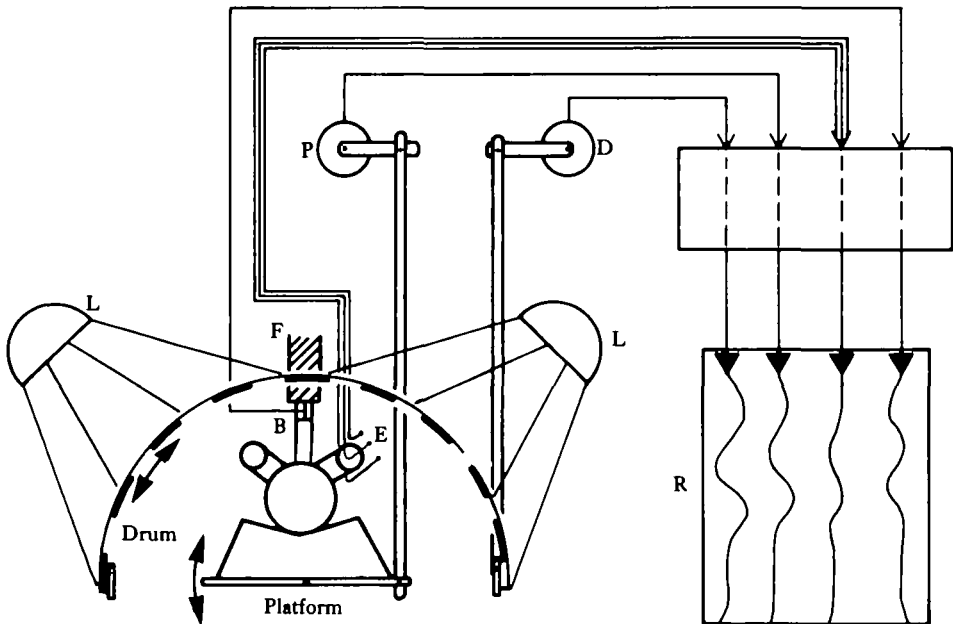


Fig. 1. The animal is held by a fixed bar (B) glued to its carapace, and stands on a pivoted platform. A striped half cylinder is mounted on a frame, which has an axis common with that of the platform, and is connected to a separate motorized drive. Lamps (L) are positioned as shown, or directly above. Outputs from potentiometers monitoring drum position (D) and platform position (P), from a force transducer in the supporting frame (F) and from an angle transducer mounted on the eye (E) are converted to voltage signals and fed to a pen recorder (R).

mounted on a narrow plastic ring which fitted firmly around the base of the outer segment without restricting vision or movement. Alternatively, caps of silicone rubber could be used either to restrict pattern vision (translucent) or to exclude all light (black). Leg forces were recorded by connecting the animal's recording frame to a strain gauge device (Grass FT.03C). All stimulus and response monitors were fed to a paper chart recorder for later analysis. In experiments with sinusoidal drum movement, measurements of response amplitude and velocity were obtained from the original records by averaging values from 6–10 cycles. Waveforms were digitized manually for Fourier analysis by computer (Mills, 1981).

RESULTS

Optokinetic responses of the eye in the roll plane

When the striped half-cylinder was rotated around the long axis of the body, both eyes followed the movement of the stripes without nystagmus until they came to rest with maintained displacements. If the drum was oscillated through an arc of less than 20°, eye movements were also continuous, and the amplitude of their excursions provided a suitable measure of tracking performance. This may not represent the maximum performance of the optokinetic system, because of the limited extent of the striped pattern in the visual field.

The strength of coupling between the two eyes in optokinetic tracking was

measured in this way. When the measured eye alone viewed the striped drum the response was reduced by 30–40 % compared with its value with both eyes viewing (Fig. 2A, B). When the other eye provided the only visual input, the movement of the capped and measured eye was reduced to approximately 50 % (Fig. 2C). These results indicate that a contralateral optokinetic drive exists, but it is weaker than the ipsilateral effect.

Responses of the eyestalk to trapezoid movements of the striped drum were investigated with both eyes seeing. For stimulus arcs up to 20° , eye movement closely followed drum movement with an amplitude gain approaching 1 (Fig. 3A). The eye then maintained its positional relationship to the stripes as long as the drum remained displaced. This property distinguishes these visually-evoked responses from those elicited by leg proprioceptor stimulation, which display a distinct phaso-tonic form (Fig. 3B, C; cf. Neil & Schöne, 1979).

Frequency response characteristics

Using sinusoidal drum movements through a 20° arc, the optokinetic response in the roll plane was tested over four decades of frequency. Above 0.05 Hz the eye

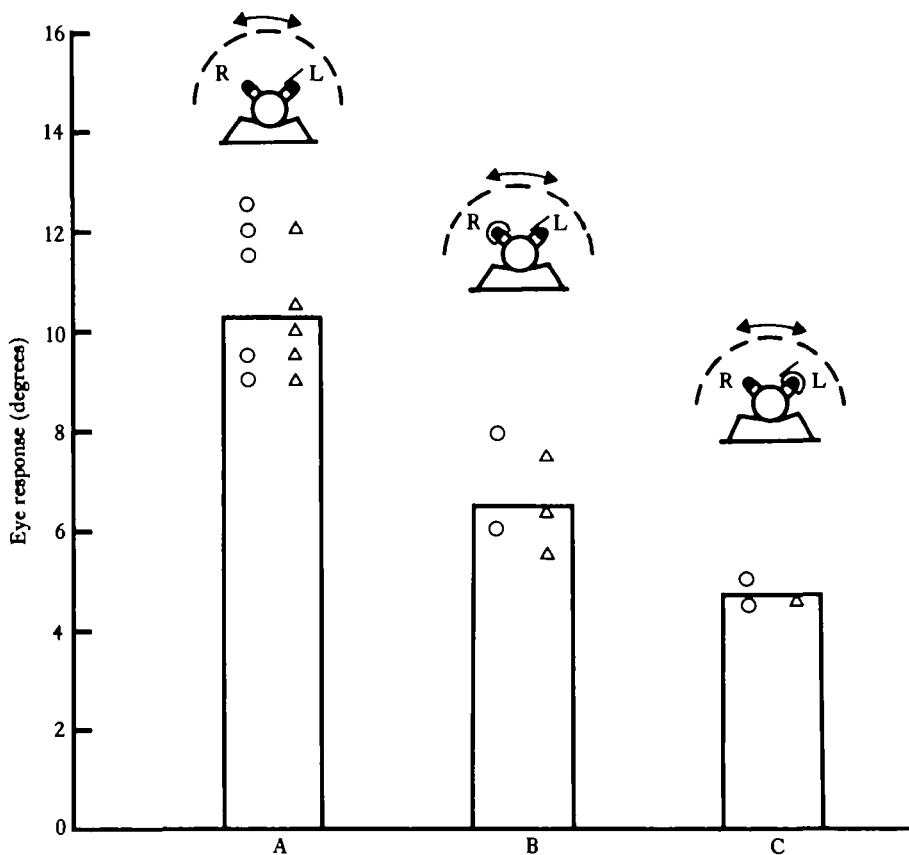


Fig. 2. Response of the left eye (measured as peak-to-peak amplitude in degrees) to sinusoidal oscillation of the drum (20° peak-to-peak amplitude, 0.06 Hz) under different viewing conditions. (A) Both eyes see. (B) Left (monitored) eye sees, right eye blinded with cap. (C) Left (monitored) eye blinded with cap, right eye sees. Results from two animals.

response was both small and strongly habituating, declining sharply after several cycles (Fig. 4A, B), until eye movement in many cases ceased completely (see Fig. 11B2). This habituation was not seen at lower frequencies, where the eye continued to follow the stripes with a constant tracking performance for as long as the stimulus was presented (Fig. 4C, D). The optokinetic system also displayed less predictable changes in responsiveness. Novel mechanical stimuli often induced transient increases in tracking gain (Fig. 4E) which were accompanied by active movements of the legs. Similar effects occurred apparently spontaneously during periods of increased arousal (Fig. 4F).

Amplitude gain increased steadily with decreasing frequency until it reached a value close to unity at 0.01 Hz (Fig. 5). This level of performance was maintained down to the lowest frequency tested, 0.0002 Hz, at which the maximum velocity of stripe movement was $0.012^{\circ}\text{s}^{-1}$.

The effect of light intensity

The amplitude of the optokinetic response remained almost constant as the light intensity was reduced (with neutral density filters) by three log units from 50 lx, until it failed completely at levels below 0.05 lx (Fig. 6). However, if the animal was kept at this light level while the drum continued to oscillate, the response showed a consistent recovery over several minutes to levels which equalled, or sometimes exceeded,

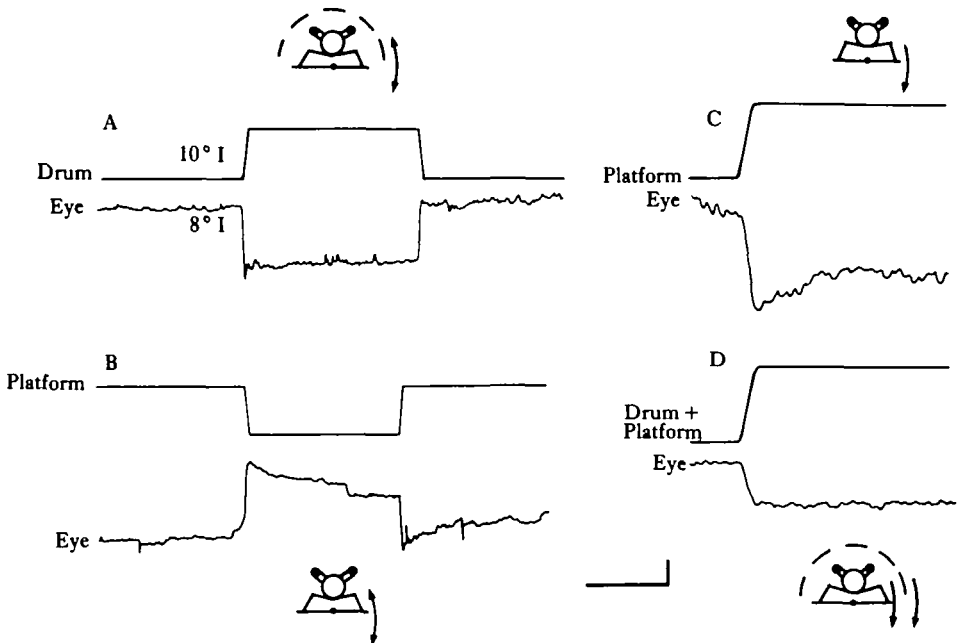


Fig. 3. Responses of left eye to trapezoid movements of drum and platform. (A) Drum alone. (B, C) Platform alone (i.e. in darkness). (D) Drum and platform together. Record pairs A, B and C, D are from separate experimental sequences. Scale bars: for drum and platform = 10° , for eye = 8° , time = 60 s in A, B; 15 s in C, D. Note the change in both shape and amplitude of the response in (D) when the visual stimulus is combined with the platform movement. Upward movement of the traces represents lowering of the left side of the platform, downward movement of stripes over the left eye, and upward movement of the left eye.

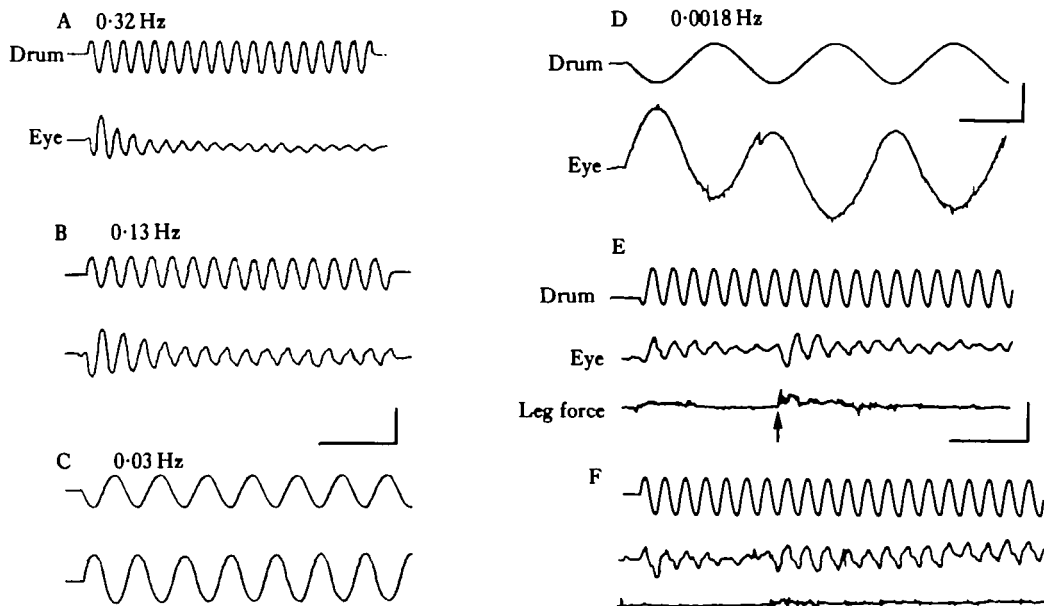


Fig. 4. Responses of left eye to sinusoidal oscillation of the striped drum at different frequencies. (A) 0.32 Hz; (B) 0.13 Hz; (C) 0.03 Hz; (D) 0.0018 Hz. (A-C) are from the same experimental sequence; (D) shows the response of a different animal. (E, F) Abrupt changes in response amplitude induced by mechanical stimulus (arrow in E), or by a spontaneous change in the arousal state (F). Force records demonstrate that these changes are accompanied by active leg movements. Scale bars: for drum = 20° , for eye = 14.5° in (A-C), 9° in (D) and 10° in (E, F), for leg counterforce = 150 g; time = 15 s in (A), 30 s in (B), 60 s in (C, E, F) and 5 min in (D). Polarity of traces in (A-D) as in Fig. 3. In (E, F) upward movement of traces represents downward movement of stripes over left eye, lowering of left eye and negative leg counterforce onto left side of platform.

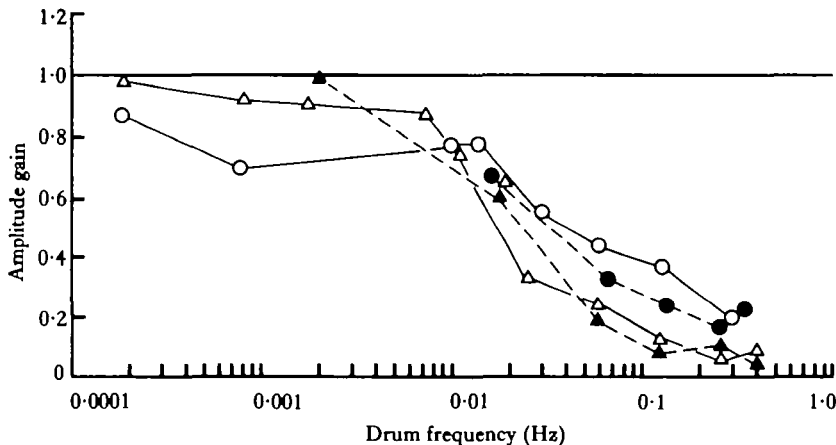


Fig. 5. Amplitude gain (maximum response amplitude/maximum stimulus amplitude) of eye response at different frequencies of striped drum oscillation (amplitude 20° peak-to-peak). Response curves for four different animals.

those found at higher light intensities (Fig. 6A-C). This adaptation process to low luminance could also be demonstrated in the experimental condition in which stationary stripes antagonized the eye response, mediated by leg proprioceptors, to a moving platform. Eye movement was completely suppressed in the presence of a stationary visual field. This effect persisted with decreasing illuminance, until at 0.05 lx the eye response

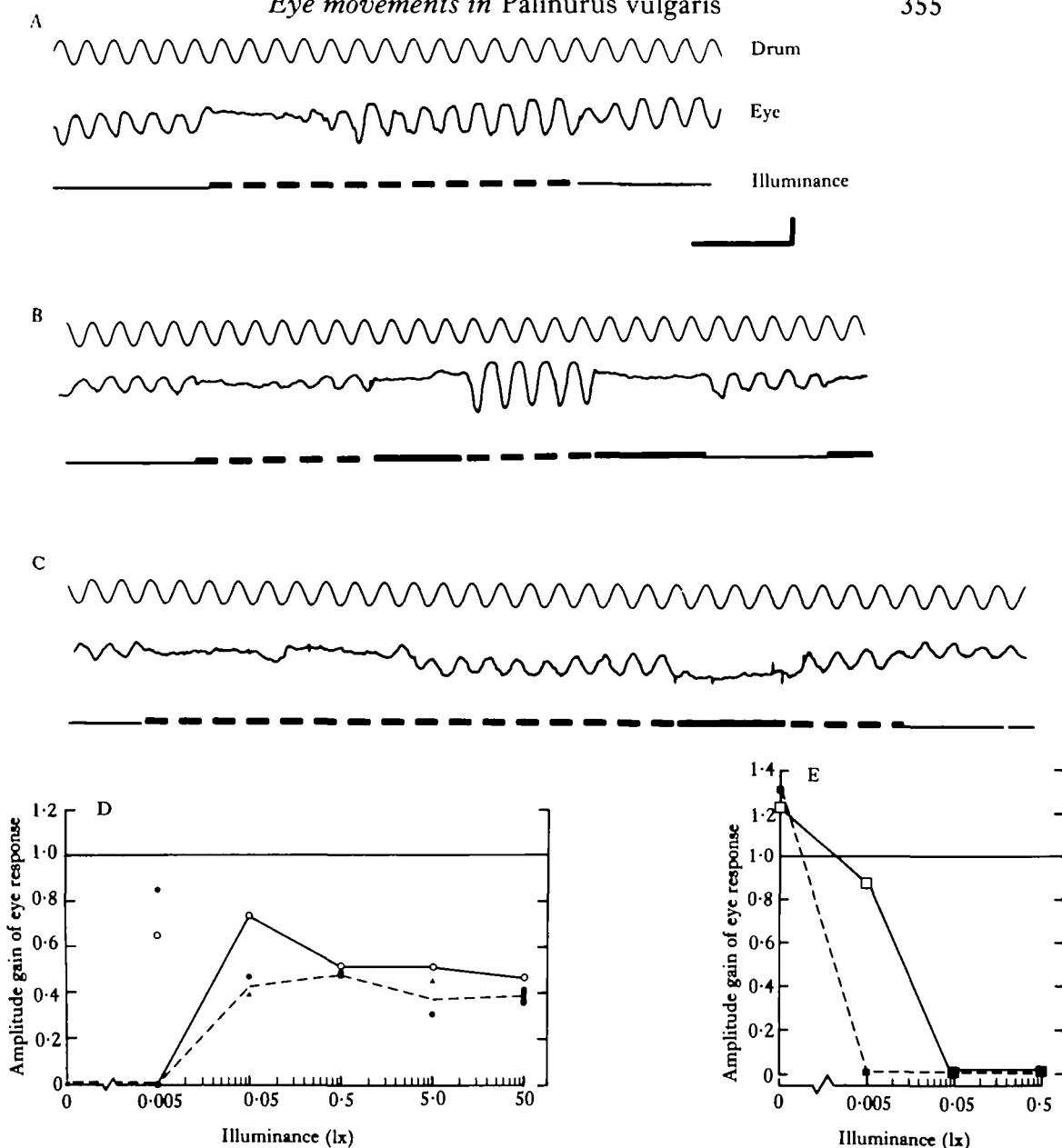


Fig. 6. The effect of irradiance level on the optokinetic response. (A–C) Responses of three different animals to the oscillating drum at two levels of illuminance, 50 lx (—) and 0.05 lx (---), and in darkness (—). Note the rate of recovery of the response at 0.05 lx, and the effect on this rate of an interposed dark period (B). Scale bars: for drum = 20°, for eye = 12° in (A), 9.5° in (B) and 14° in (C); time = 120 s. Polarity of traces as in Fig. 3. (D) Plot of amplitude gain (output/input) of eye response against irradiance level. Open and closed symbols represent responses of two different animals. In the latter case measurements were obtained both for steps of increasing illuminance (●) and for steps of decreasing illuminance (▲). Response curves are constructed through the values obtained immediately following changes in illuminance level. These differed from values obtained 5 min later only at 0.05 lx (isolated symbols). (E) The influence of a stationary striped drum on the eye response to platform oscillation at different illuminance levels. Amplitude gain curves are plotted separately for the response immediately following changes in illuminance (□—□) and the response 5 min later (■—■).

to leg input appeared with an amplitude approaching that found in the dark (Fig. 6E). After several minutes at this light level, however, eye movement was again abolished.

To show that irradiance was a stimulus separable from the optokinetic stimulus of the high-contrast stripes, the striped drum was replaced by a translucent drum which transmitted light, but not pattern, to the upper half of the visual field. Translucent panels in front, and a translucent platform below, minimized the effect of stationary edges in the animal's field of view. Under these conditions movements of the drum itself elicit no optokinetic response (Schöne *et al.* 1983). The effect of the unpatterned visual stimulus on the eye response was tested in combination experiments with the platform stimulus. The amplitude of eye movement was much reduced, compared with the response in darkness (Fig. 7C, F).

To test for the possibility that stationary edges in the visual field were responsible for this effect, the following experiment was performed. The eyes were covered with translucent caps of silicone rubber, which transmitted light but not pattern. Their effectiveness was checked by measuring the eye response to the moving striped drum. With the caps on, response amplitude was reduced by more than 80 %, compared with that obtained with both eyes seeing (Fig. 7A, B). With the combination of translucent drum and platform, however, the inhibitory effect of the visual stimulus was still significant (Fig. 7D, F), despite a reduced amount of light reaching the eyes through

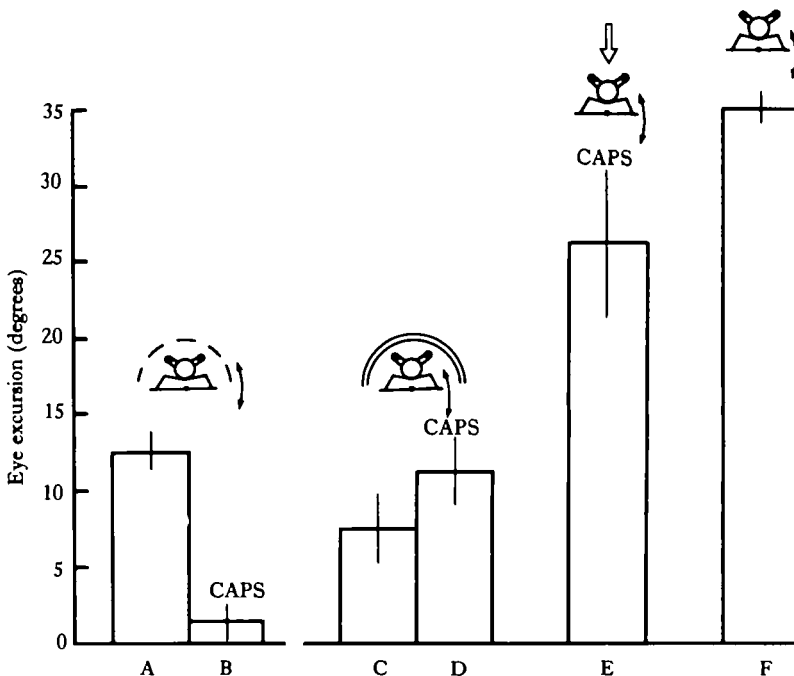


Fig. 7. Responses of the left eye (measured as peak-to-peak amplitude in degrees) to sinusoidal oscillation (20° peak-to-peak, 0.03 Hz, of the striped drum (A, B) or platform (C–F) under different viewing conditions. (C, D) Translucent drum illuminated from above. (E) Overhead light source (open arrow), no drum. (F) Darkness. In (A, C) both eyes are uncovered, and in (B, D, E) both eyes are covered with caps of translucent silicone rubber (CAPS). The height of each column represents the mean value from ten cycles of stimulation in a single experimental sequence; the vertical lines indicate two standard deviations.

the translucent caps. Furthermore, this inhibition was reduced when the drum was removed, revealing the point light source above, but reducing the area of brightness in the upper visual field (Fig. 7E). This procedure would also, potentially, introduce more stationary edges into the animal's field of view. We therefore conclude that under the translucent drum the distribution of light over the eye is responsible for the observed effects, that these are proportional to the number of ommatidia stimulated, and that optokinetic responses to any remaining edges in the field of view play no

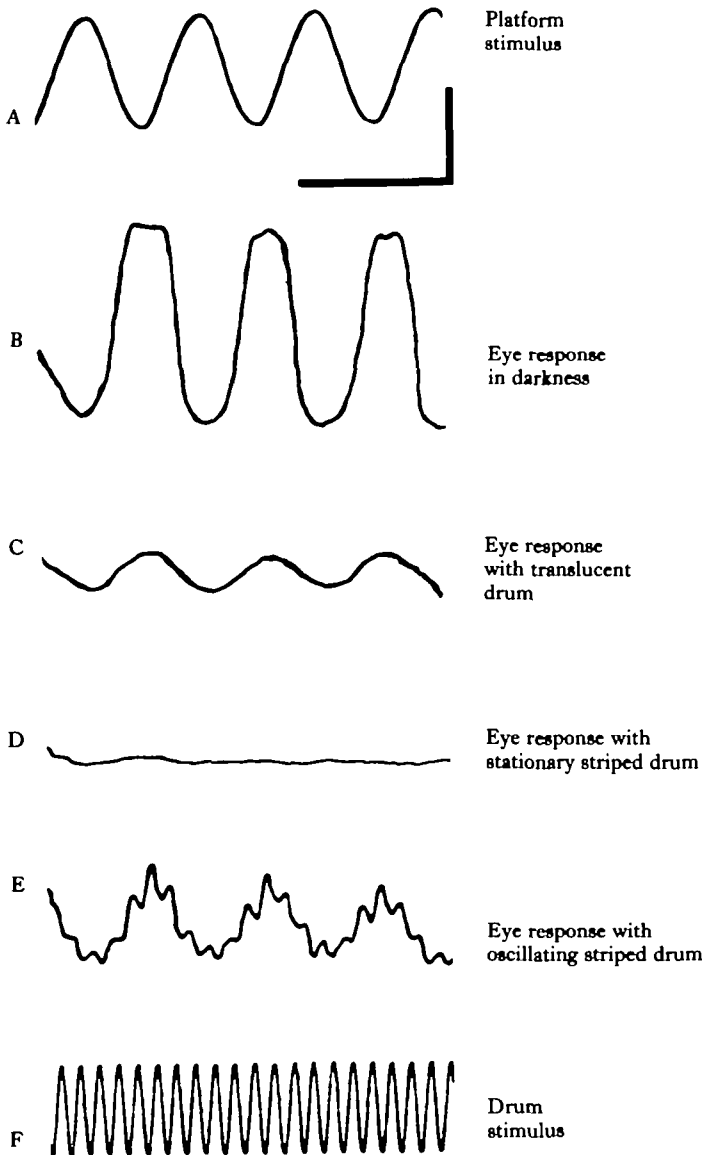


Fig. 8. Composite record from an experimental sequence in which platform oscillation (A) was combined with a number of different visual stimuli. (B-E) Eye responses, (F) striped drum (refers to trace E only). (B) Darkness. (C) Illuminated translucent drum (50 lx). (D) Stationary striped drum. (E) Oscillating striped drum. Scale bars: for platform and drum = 20°, for eye = 23°; time = 60 s. Polarity of traces as in Fig. 3.

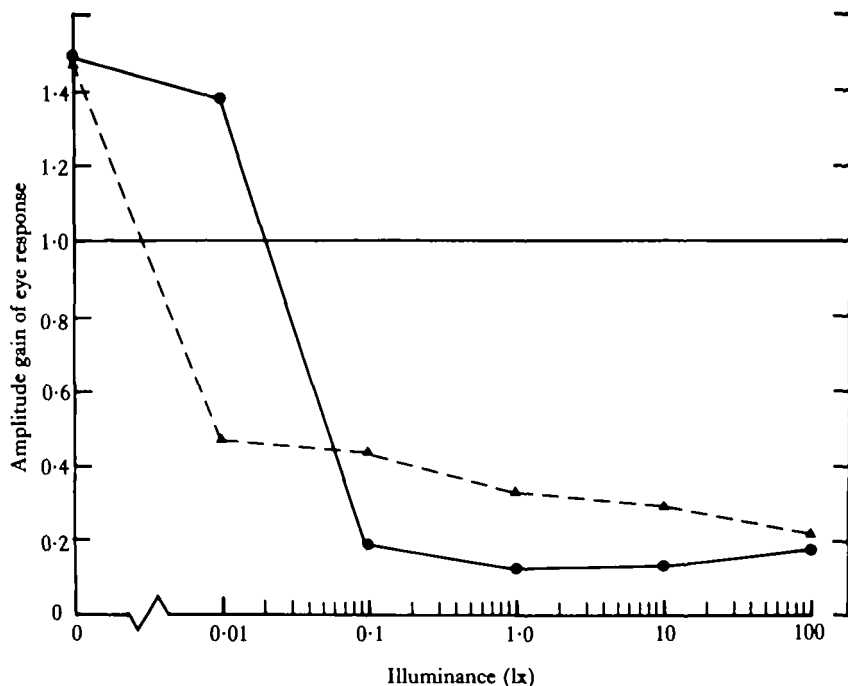


Fig. 9. Eye response to platform oscillation (20° peak-to-peak, 0.06 Hz) at different illuminance levels under a translucent drum. Amplitude gain curves are plotted separately for responses immediately following changes in illuminance (●—●) and responses 5 min later (▲—▲).

significant part. The involvement of this second visual factor may underlie other observed effects: thus when the response to rapidly oscillating stripes has faded, the eye response to simultaneously imposed platform movement under the legs remains suppressed (Fig. 11B).

The two visual inputs appeared to interact destructively. By oscillating the striped drum at a high frequency which sustained the optokinetic response, in combination with a platform tilt at lower frequency, it was found that the inhibition of the proprioceptive eye reflex was less than that produced by a translucent drum transmitting the same illuminance (Fig. 8).

The effect of irradiance level on the strength of the second visual factor was measured in experiments under the translucent drum. At the higher light intensities (from 100 lx to 0.5 lx) the eye response to platform oscillation was reduced, although not completely abolished (Fig. 9). At 0.1 lx, however, there was a difference between the response on immediate presentation, when it appeared in a virtually complete

Fig. 10. Bode plots of the amplitude gain and phase position of the eye response to striped drum oscillation (■—■, A, B), platform oscillation in darkness (●—●, C, D), drum and platform oscillation at the same frequency in a synergistic phase combination, i.e. in phase (□—□, A, B) and drum and platform oscillation at the same frequency in an antagonistic phase combination, i.e. antiphase (○—○, C, D). (A, C) Amplitude gain against oscillation frequency. (B, D) Response phase (re. stimulus cycle) against oscillation frequency. In (B) phase-lock to drum and platform = 0; in (D) phase-lock to drum = 1, phase lock to platform = 0.

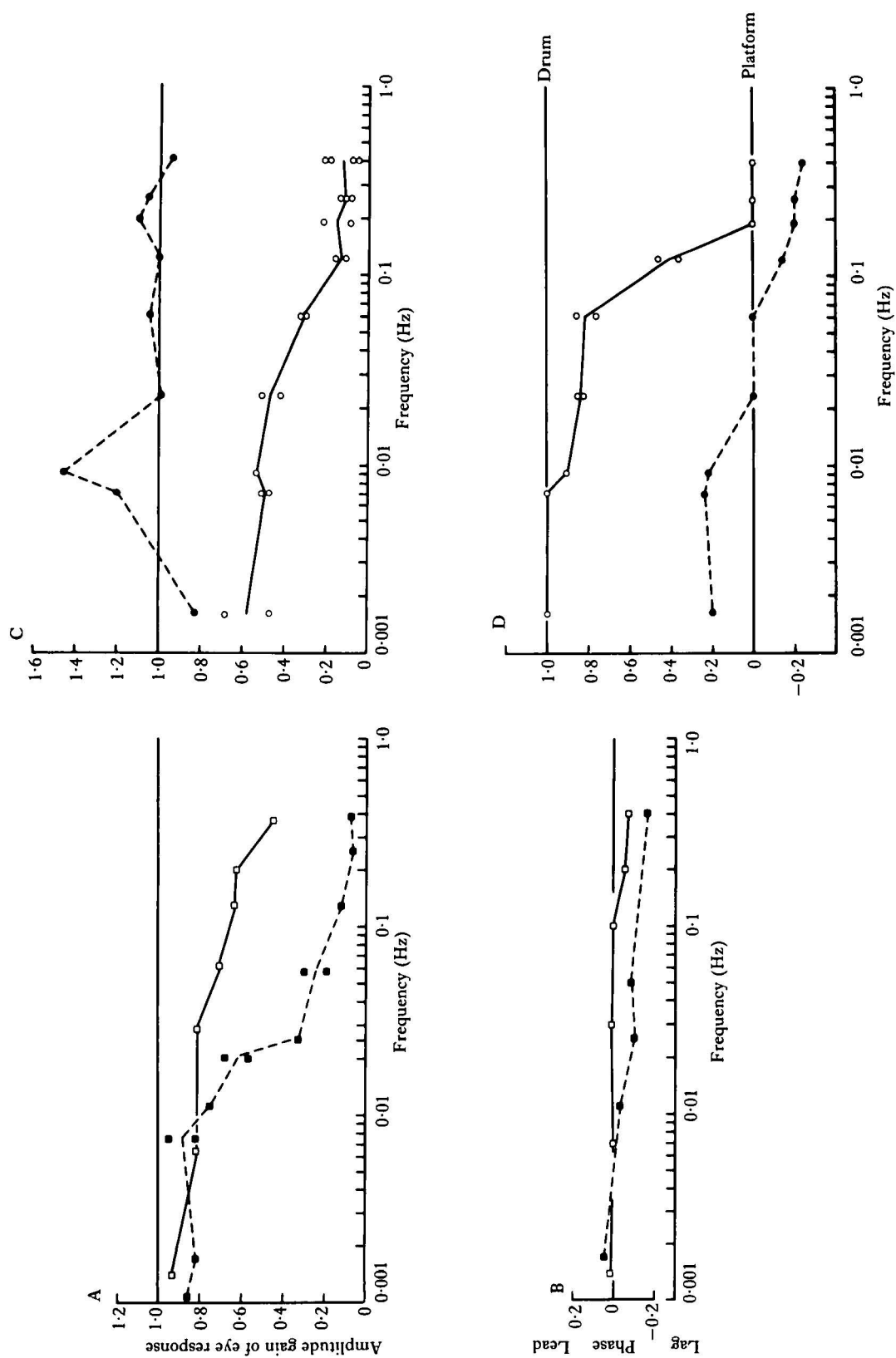
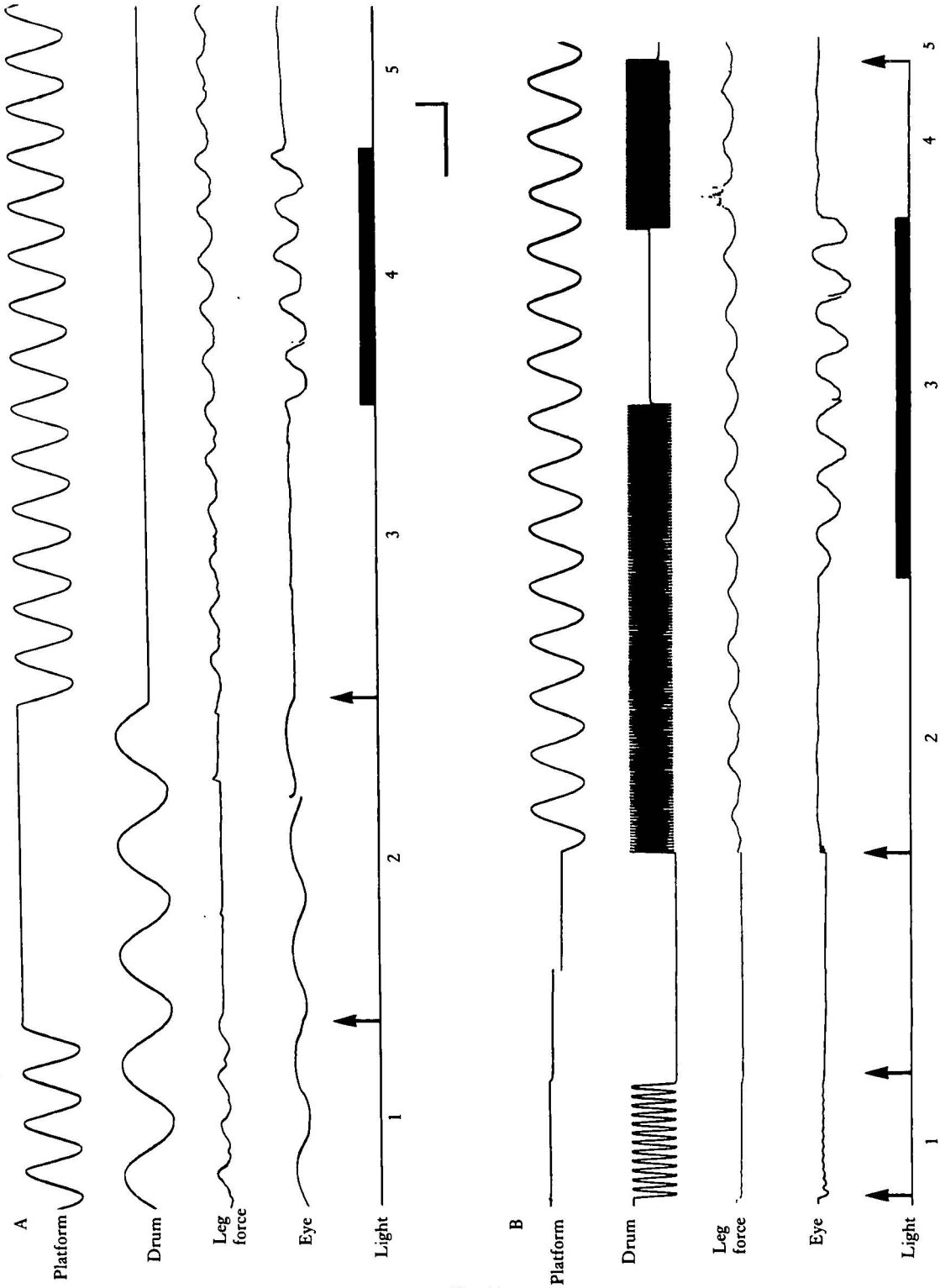


Fig. 10



form (Fig. 9, solid line), and after a period of several minutes, when it was again markedly suppressed (Fig. 9, dashed line).

Interaction of vision and proprioceptive input

When movements of the striped drum and platform were presented in a phase relationship promoting synergistic reflex effects, a major influence on the eye response was the gain-limiting property of the optokinetic system. This was expressed in the reduced gain of the reflex, compared to that obtained in the dark, in the low frequency range (Fig. 10A, C).

When the two stimuli were presented in an antiphase combination, the amplitude of the eye response showed a general reduction as frequency was increased, compared to that elicited by platform movement in the dark (Fig. 10C). The nature of these responses is made more apparent when their phase positions relative to the stimuli are taken into account. Below 0.06 Hz the response had a phase close to that of the drum, while in the high frequency range it was in phase with the platform, but with a much reduced amplitude (Fig. 10D). The dominance of the optokinetic system at low frequency is therefore confirmed, since it now induces a large counter-movement of the eye against the direction dictated by the leg proprioceptor input.

With different frequencies and different relative strengths for the separate stimuli, interaction at all relative phase positions could be studied. We used an intermediate frequency of platform oscillation in combination with drum movements at both higher and lower frequencies. When the frequency difference was large, clear-cut effects were seen: the eye followed the drum if its frequency was low (Fig. 11A), but failed to follow either drum or platform if drum frequency was high (Fig. 11B). When the frequency difference between the drum and platform was small (Figs 8, 12A), the compound waveform of the eye response curve was difficult to interpret. However, Fast Fourier Transform (FFT) analysis of these waveforms revealed that they were composed exclusively of periodic components corresponding to the two input frequencies, and no others (Fig. 12B). An estimate of the relative weighting of the two inputs was provided by the area of each peak in the FFT plot, and was separately obtained by generating a matched waveform from the two input monitoring signals (Fig. 12C). Overall, these results indicate that at the chosen platform frequency, 0.02 Hz, weighting changes steadily with drum frequency from completely to the drum at 0.01 Hz to completely to the platform at 0.25 Hz.

Fig. 11. Eye response and leg counterforce to combinations of platform and drum oscillation at unequal frequencies. (A) Platform oscillation at 0.02 Hz, drum oscillation at 0.01 Hz. The combined stimulus (1) induces eye movements which are closely similar to those which are elicited by the visual stimulus alone (2). Large eye movements to platform oscillation appear in darkness (4), but are completely suppressed when the stationary drum is illuminated (3, 5). The strength of the leg counterforce appears to depend to some extent on the presence or absence of the visual stimulus (compare 3, 4, 5). (B) Platform oscillation at 0.02 Hz, drum oscillation at 0.25 Hz (0.12 Hz in 1). The high-frequency visual stimuli induce a rapidly fading optokinetic response (1) but suppress the response to the simultaneous stimulus of platform movement (2, 4), as does stationary stripes (5). In darkness (3) a large eye response to platform oscillation appears. The leg counterforce appears not to be modified by the various visual stimuli. Scale bars: for platform = 10°, for eye = 25°, for leg counterforce = 200 g; time = 60 s. Thick bars on bottom traces indicate periods of darkness. Upward movement of traces represents lowering of left side of platform, downward movement of stripes over left eye, negative leg counterforce onto left side of platform and downward movement of left eye.

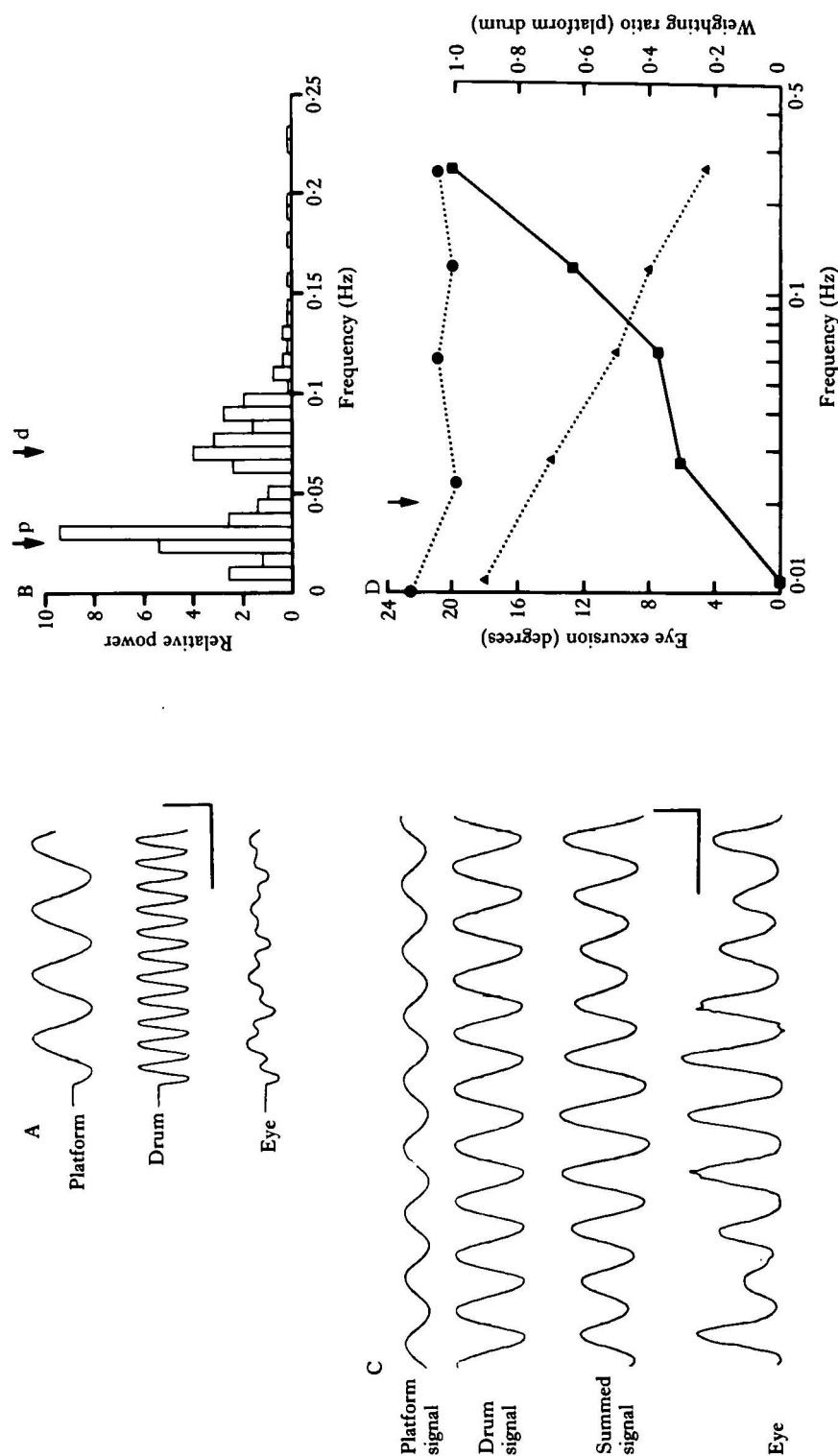


Fig. 12. Relative weighting of sensory inputs produced by combined drum and platform oscillation at unequal frequencies. (A) Records obtained when the two stimuli approximate in frequency: platform = 0.25 Hz, drum = 0.07 Hz. Scale bars: for platform and drum = 20°, for eye = 29°; time = 60 s. Polarity of traces as in Fig. 10. (B) Analysis of the eye response waveform shown in (A) by Fast Fourier Transform. Arrows indicate the input frequencies of the platform (p) and drum (d) stimuli. (C) Record from a wave-matching experiment. Combination of platform oscillation at 0.020 Hz and drum oscillation at 0.017 Hz, with equal and constant amplitude throughout (20° peak-to-peak). Two signals at the frequencies of the platform and drum, and initially of equal size, have been summed electronically to produce the waveform shown in the third trace. The platform signal has been adjusted until this summed waveform matches as closely as possible that of the eye response. The ratio of the signal amplitudes then represents the relative weighting of the sensory inputs in dictating eye movement. Scale bars: for eye = 10°; time = 60 s. (D) Plot of the relative weighting of sensory inputs (right hand axis, ■—■) in one animal produced by the platform and drum against the frequency of drum oscillation. Platform oscillation was constant at 0.02 Hz (arrow). Weighting values have been calculated as described in (C). Also plotted are the eye response amplitudes in this animal (left hand axis) to the separate presentation of the platform stimulus (●—●) and the moving drum (▲—▲) over the same frequency range.

DISCUSSION

The optokinetic response

The major features of the optokinetic reflex system of the spiny lobster in the vertical plane are consistent with those found in the other decapod crustaceans so far investigated (reviewed by Neil, 1982). Coupling between the two eyes is stronger than in crayfish (Hisada *et al.* 1969) but comparable to that for horizontal movements in the crab *Carcinus* (Barnes & Horridge, 1969; Sandeman, Erber & Kien, 1975). The strength of this bilateral coupling may vary with stimulus conditions, however, for York *et al.* (1972) report that the eyes of the spiny lobster *Panulirus* may move with a high degree of independence in a less uniform visual environment. The closed-loop frequency response (Fig. 5) typifies a system which normally operates with negative feedback control (Horridge, 1966). The lower threshold for movement detection by the visual system was not reached in our experiments, but must lie below 0.01°s^{-1} (Fig. 5). The performance of the optokinetic tracking system in *Palinurus* may therefore approach that found in *Carcinus* (Horridge, 1966).

Response to the irradiance gradient

The identification of a second visual response in *Palinurus* to the illuminance *per se* (Schöne *et al.* 1983) is confirmed here (Fig. 10). In addition, we have demonstrated that there is an interaction between this visual system and the optokinetic system, which under some circumstances can be antagonistic. The separate existence in crustaceans of visual systems attuned to overall light distribution and wide-field movement has been demonstrated both by behavioural measures (Wehner, 1979; Schöne, 1980) and in certain species by electrophysiological techniques (*Panulirus*: York & Wiersma, 1975; *Procambarus*: Wiersma & Oberjat, 1968; Higuchi, 1973; Higuchi & Hisada, 1973). In the crayfish, light entering the eye causes reflex excitation of muscles which lift the eyestalk (Higuchi, 1973) through a motor pathway which may be separate from that for other eye reflexes (Mellon & Lorton, 1977).

In considering the apparent dominance of vision over the proprioceptive inputs (Figs 6, 8, 10, 11) it must be recognized that the irradiance gradient contributes a strong stabilizing influence on eye position (Figs 7, 8, 9). This is probably not through a general inhibition, but is more likely to be due to its action as a stable directional cue. Thus, under appropriate conditions this visual stimulus can enhance the eye response to mechanosensory stimulation, rather than suppress it (Schöne *et al.* 1983, Fig. 8).

Multisensory interaction

In order to reveal the nature of the interaction between the optokinetic component of the visual system and leg proprioceptive inputs it is necessary either to create a uniform field of illumination around the optokinetic stimulus (Hisada *et al.* 1969; Neil, 1975), or, as here, to produce movements of both the optokinetic and platform stimuli relative to a stationary light gradient (Figs 10, 11, 12). This experimental arrangement is, of course, completely artificial, the natural relationship consisting of in phase stimulation of both visual subsystems, and of leg proprioceptor and statocyst

inputs. However it demonstrates essential features of the combined control system, the most obvious of which is an extension of the linear range of the eye responses through the individual contributions of the optokinetic and leg proprioceptive systems tuned to low-frequency and high-frequency ranges respectively. This is a common feature of related interactions in many different animals (crab: Sandeman, 1977; crayfish: Olivo & Mellon, 1980; rabbit: Collewyn, 1981; monkey: Waespe, Henn & Isoviita, 1980).

It has often been suggested that multisensory interaction in the control of crustacean eye movements is based upon a simple algebraic summation of the inputs from the different sensory systems involved (Fay, 1973; Mellon & Lorton, 1977; Olivo & Jazak, 1980). However, our results obtained over a wide frequency range clearly show that this is an inadequate explanation, which ignores the differences between the operation of the closed-loop optokinetic system and the open-loop proprioceptive system. Responses to low-frequency wide-field optokinetic stimuli are dominant, in the face of both antiphase platform movement and a conflicting stable light gradient (Figs 10, 11, 12). A similar effect has recently been described by Varju & Sandeman (1982) in the crab *Leptograpsus*.

Visual dark adaptation

Significantly, we find that although clearly distinct, the separate visual subsystems in *Palinurus* are affected in similar ways by reduced illuminance. They both demonstrate a threshold sensitivity and subsequent adaptation which have closely similar characteristics (Figs 6, 9), and we interpret this common effect as a strong indication that the adaptation process takes place at a site peripheral to the separate neural integration networks. The time course of visual adaptation is consistent with that reported for screening pigment migration in a number of different crustacean species (de Bruin & Crisp, 1957; Olivo & Larsen, 1978). Such pigment movements would have the effect of increasing the sensitivity of the eye, since the exposed tapetum would reflect light back onto the rhabdoms, increasing quantum capture. The necessary concomitant of this, a loss of acuity, may well not have limited the responses under our experimental conditions with wide-field stripes, although this has not been directly tested. The behaviour of screening pigments in crustacean eyes is complex (Autrum, 1979), being dominated in many cases by intrinsic circadian rhythms (Leggett & Stavenga, 1981). In the spiny lobster, *Panulirus interruptus*, it is not possible to cause light adaptation of the night eye, or dark adaptation of the day eye (Meyer-Rochow, 1975). Our results suggest that for *Palinurus* this question must remain open until a more thorough analysis of screening pigment movement in relation to both the day/night cycle, and to the behavioural responses at different light intensities has been performed.

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