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Eye-Scanning during Walking in the Crab *Leptograpsus variegatus*

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Summary. The eyes of the crab *Leptograpsus variegatus* scan continually when the animal walks. The scanning movements are in the horizontal plane, have an amplitude of between 0.1° and 0.3° and a frequency of about 6 Hz if the animal is surrounded by a bright, contrasting visual field. The scanning movements are abolished if the animal is placed in the dark, or blinded. During scanning the two eyes are predominantly in phase with each other. It is proposed that the scanning is the result of a general increase of activity in the oculomotor neurons during walking, which causes the eyes to oscillate at a frequency which is set by the properties of the optokinetic feedback system. It is suggested that the main function of scanning is to prevent visual adaptation.

Introduction

Much of the work on the eye movement system of the crab has been confined to the investigation of compensatory eye movements which are evoked by visual targets moving around the animal or angular accelerations applied to the body of the animal (Sandeman, 1978). In these studies the animals were usually suspended in clamps and their legs were either removed or not allowed to contact the substrate. The experiments have provided a good idea of how the eye movements are controlled by a visual feedback system, backed up by the statocyst system which can detect angular accelerations but which is apparently without feedback.

There is far less information about the eye movements which are made by an animal when it moves itself. An early report describes relatively slow back and forth movements of the eyes of *Carcinus* which were seen when that animal walked sideways (Bethe, 1897). The eyes of *Carcinus* also drift, tremor and undergo saccades when the animal is suspended above the substrate (Sandeman, 1963; Barnes and Horridge, 1969). These eye movements are similar to those of the vertebrates and have therefore been given the same descriptive terms. A fourth type of eye movement, called eye waving, has been described for *Carcinus*. These eye movements were observed when a suspended animal waved its legs about and are described as oscillations having a peak amplitude of 0.1 to 2 degrees and a frequency of 2 to 3 Hz. Eye waving takes place predominantly in the horizontal plane and like the eye tremor is probably brought about by phasic activity in the eye muscles (Horridge and Burrows, 1968). In eye waving the two eyes are reported to move independently of each other (Barnes and Horridge, 1969).

In this paper I report the observation of eye scanning movements which are made by the crab *Leptograpsus* when it is allowed to walk about on a polystyrene ball. I have found that the scanning movements of the eyes in *Leptograpsus* are 0.1° to 0.3° of arc and have a repeat frequency of 5 to 6 Hz if the animal is surrounded by a high contrast visual field. The movements of the two eyes are largely in phase with one another. The frequency of the scanning movements is affected by the number of contrasting stripes in the visual field and the highest frequency of scanning which has been observed can be related to the latency of the optokinetic response. It is concluded that during walking in *Leptograpsus* there is a continual injection of neural noise into the optokinetic system which responds with a maintained oscillation, the frequency of which is determined by the delay in its feedback loop. The effect of eye scanning on the spatial resolution of the crab and the adaptation of the visual system to stabilized images is discussed.

Material and Methods

The Australian rock crab, *Leptograpsus variegatus*, was used for all experiments. The animals were caught locally and kept in sea water aquaria in the laboratory.

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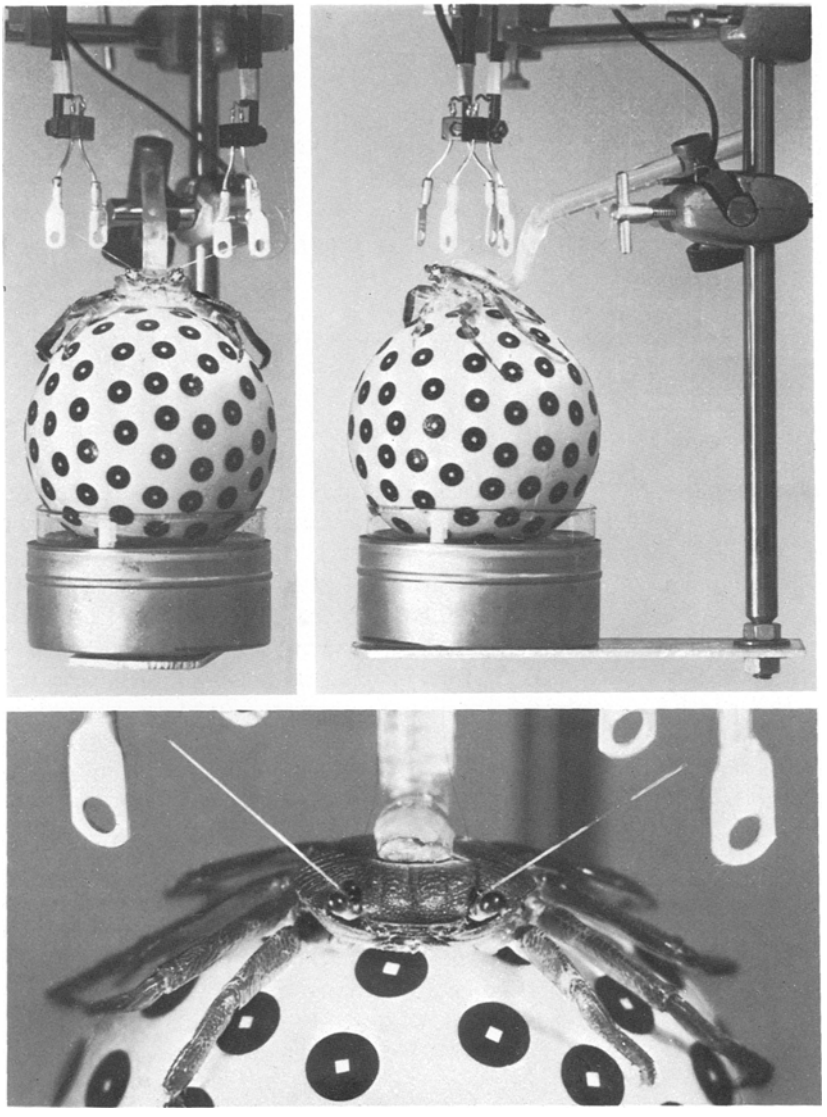

Fig. 1. Experimental set-up used to measure eye movements of the crab walking on a polystyrene ball, seen from front and from side. Animal glued by its back to the perspex rod. Polystyrene ball partially supported by water in the glass bowl beneath it. Lower picture shows the glass fibres on eyes of the crab, fine silver wires leading to the base of the fibres and up inside them. Plates positioned on either side of the fibres are connected to separate differential amplifiers

Experimental animals were induced to autotomise their chelipeds before glueing a supporting rod to their backs. They were lowered onto a polystyrene ball, 10 cm in diameter, which was supported in a glass dish partly filled with water (Fig. 1). The amount of water in the dish was controlled so that the weight of the crab forced the ball down to rest lightly on the smooth rim of the dish. The animal was then fastened in this position and could walk the ball around in all directions. The movement of the ball was detected by placing black spots on it and allowing these to pass a single photosensitive diode.

The eye movements were detected with a capacitative position sensing device (Sandeman, 1968). Hollow glass fibres glued to the eyes had thin insulated wires within them and these were connected to a signal generator supplying a 40 kHz sine wave. The signal radiated from the fibres was detected by plates on either side of them which were connected to differential amplifiers (Fig. 1). The advantage of this device over photo electric systems is that relatively large eye movements do not move the fibre out of the range of the detector. For the observation of the small eye movements described in this paper, the sensing device was A.C. coupled to the recording system so that the large eye movements were excluded from the record.

The crab with its supporting ball and eye movement detection system was placed in the centre of an arena into which black vertical stripes could be introduced without moving the animal. The black stripes subtended a vertical angle at the crab of 80°; 40° below and 40° above the horizontal through the eye. The width of the stripes was 10° measured at the eye. The light level in the arena without stripes was 55 cd/m^2.

The animals could be induced to walk by gently brushing their legs but they often began walking by themselves and would walk at a regular pace for 1 to 3 min. Frightened animals will either sit quite still or make short rapid runs on the ball. The eye movements during such runs are large and rapid but do not form part of this study.

In one set of experiments the crabs were allowed to rotate about their vertical axes. This was achieved by mounting the crab and the eye movement detection device on a freely turning vertical spindle. The ball beneath the animal was not supported by water in this instance and the greater friction between the ball and the

dish meant that for rotational movements the animal turned its own body in relation to the visual environment.

A test of the veracity of the eye-movement detection system was made by glueing the eye to the carapace so that it could not move and then allowing the animal to walk. Vigorous leg movements introduced small artefacts but these were of a relatively low frequency and well below the amplitude of the smallest eye scans.

Results

1. Rapid Eye Scanning

An animal sitting quietly on top of the polystyrene ball and surrounded by a visual field containing stationary vertical stripes, would, from time to time, exhibit single or several eye scans, superimposed on a much smaller continual eye tremor. The amplitudes of the scans of the two eyes were not always the same but, where large scans occurred in one eye, they were attended by small scans of the other eye in the same direction (Fig. 2A). The scanning did not continue for more than 10 to 15 cycles before it died away, although it was often initiated again after the space of one or two cycles. Walking was accompanied by a marked and sustained oscillation of both eyes (Fig. 2B) which could continue for 2 or 3 s after the animal had stopped walking. The eye scans during walking were 0.1° to 0.3° and had a frequency of between 5 and 6 Hz. The phenomenon is remarkably consistent and has been observed in every animal which has been examined including crabs which were completely unrestrained, when the oscillations of fibres glued to their eyes could be clearly seen.

2. The Effect of Allowing Rotational Freedom

There was no observable difference in the eye scanning found in an animal free to move about its vertical axis and one which was restrained. A significant difference was found in the much larger compensatory eye movements which were made when the animal turned. If free to move the animal would move its eye rapidly in the direction in which it turned and then turn its body while the eye remained fixed relative to the stationary visual surround. This is shown in Figure 3A, where the fast phase movements of nystagmus were followed by the slow movement of the eye as the crab turned its body. A crab not free to rotate in relation to the stationary visual surround would still make the fast-phase saccade during rotational movements but the eye then stayed in this position (Fig. 3B). Placing the animal in the dark but still not allowing it rotational freedom resulted in a third type of response: the eye scanning was no longer seen and the eye drifted back and forth during walking. The fast saccades which accompanied rotation were followed by the eye drifting back to the place from which it made the fast saccade (Fig. 3C). The eye movements made by an animal in the dark were very like those made by a crab in the light with the visual feedback loop opened (Sandeman et al., 1975).

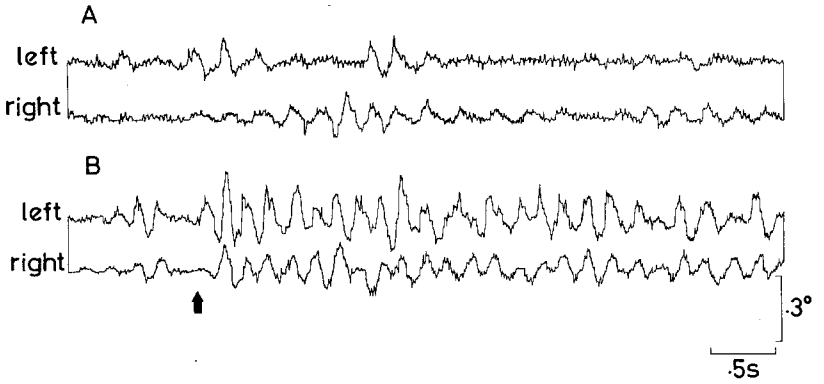

Fig. 2. A Eye tremor and scanning of left and right eyes of an animal not walking. **B** The animal begins to walk (arrow) and this is accompanied by oscillations in both eyes

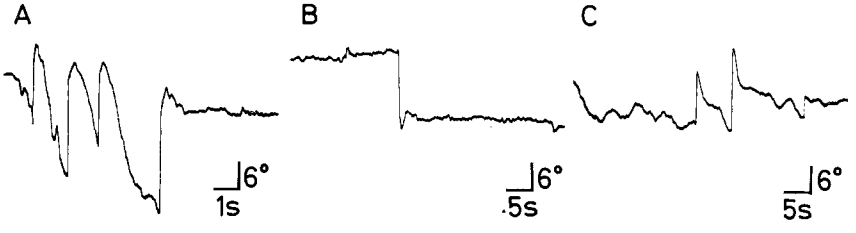

Fig. 3A–C. Fast and slow phases of rotational nystagmus when an animal was: **A** Free to rotate about its vertical axis, past a stationary pattern of stripes. **B** When rotational freedom was prevented. **C** When rotational freedom was prevented and the animal was placed in the dark

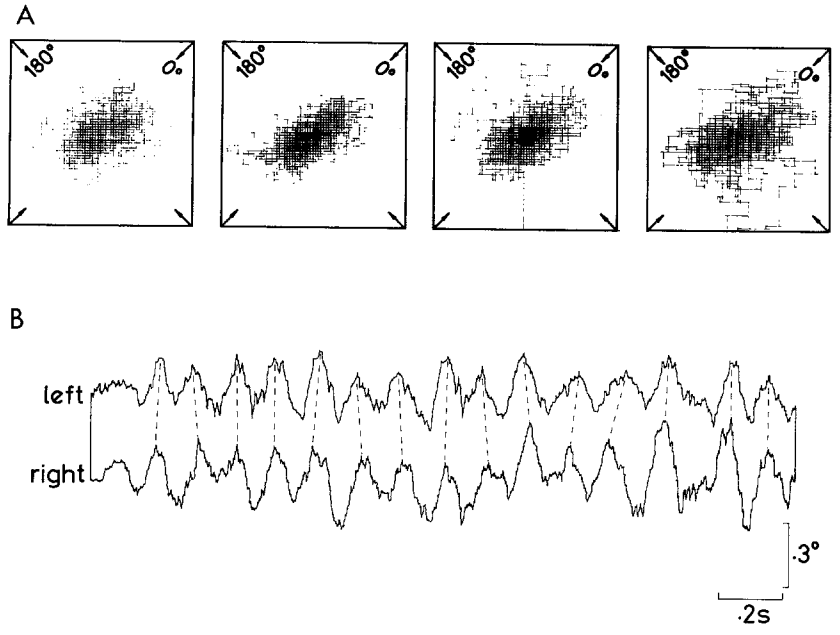

Fig. 4. A Lissajous figures obtained by plotting oscillation of one eye against the other. Each figure: results of plotting about 30 cycles. Orientation of the ellipse shows that eyes remain predominantly in phase. **B** Cycle by cycle correlation of a series of eye scans showing that individual eye scans can be matched by their shape and also that they remain loosely phase coupled

3. The Phase Relationship of the Eyes

Small eye tremor movements and eye waving in *Carcinus* are reported to be usually independent in the two eyes (Barnes and Horridge, 1969), however, during scanning in *Leptograpsus* the eyes are phase coupled.

The phase relationship of the two eyes during scanning in *Leptograpsus* was determined by plotting the responses of each eye against the other and displaying the result as a Lissajous figure (Fig. 4A). Each figure is the result of 30 consecutive eye scans recorded during sustained and regular walking. Despite the variations in amplitude which increase the scatter of the figures, the orientation of the ellipses is clearly in the direction which indicates phase coupling. Examining the scans from the two eyes on an expanded time scale and correlating them cycle by cycle confirms the above result. Irregularities in their shape and amplitude allow the individual scans to be matched and they can be seen to drift in and out of phase with one another (Fig. 4B). In some records it is possible to find the eyes moving in antiphase for one cycle (see for example half way along the trace in Fig. 2B) but this is followed by the eyes coming abruptly into phase again.

4. The Effect of Visual Feedback

The visual feedback which stabilizes the eye in relation to the surround can be altered by monocular or binocular blinding or by placing fewer contrasting objects within the visual field. An animal which could see with both eyes and was surrounded by stationary black vertical stripes, scanned with both eyes when it walked (Fig. 5A). Blinding one eye by painting it over abolished the scanning of that eye but the seeing eye was unaffected (Fig. 5B). Blinding both eyes prevented the oscillation of both and walking was accompanied only by the irregular tremor movements of the eyes and an increased drift (Fig. 5C).

The number of stripes in the visual field affects the frequency of the scanning. With no stripes in the visual field, walking was accompanied by eye scanning which had a mean frequency of 3.3 Hz (Fig. 6). It should be pointed out that the animal's field of view was not totally without detail. The bars which supported it and the detection device, the detection device itself, and the edge of the carapace around the eye socket are all edges which could have provided feedback for the visual system.

A single stripe placed in front of the animal raised the scanning frequency to 4.8 Hz and a single stripe at the side to over 5 Hz. The addition of more stripes to the visual field served to increase the frequency only slightly (just over 6 Hz for 10 stripes).

5. Eye Scanning and the Latency of the Optokinetic Response

Abruptly accelerating a striped pattern around the animal from 0 to 1°/s showed that 80 to 100 ms after the striped pattern had started to move, both eyes moved in the same direction as the pattern but faster

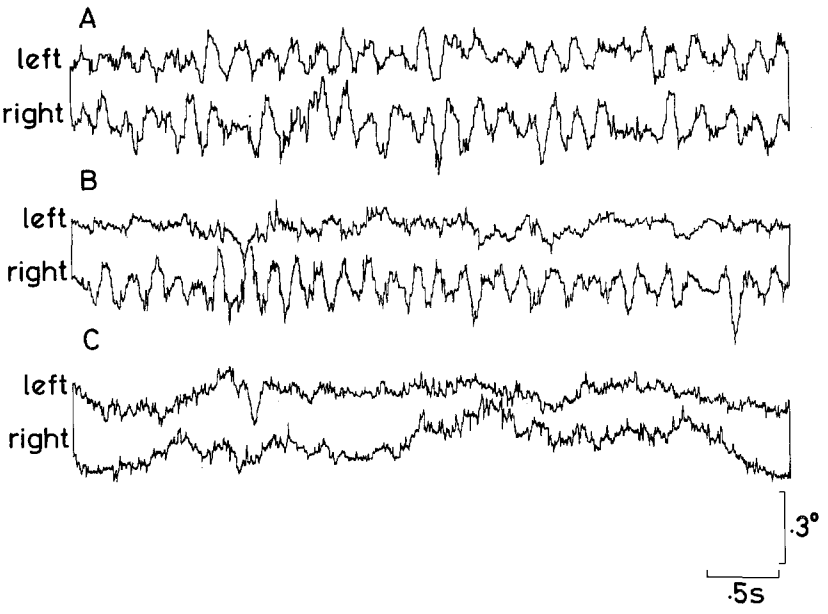

Fig. 5A–C. Effect of blinding first one and then both eyes on the eye scanning.
A Both eyes see
B Left eye is painted over
C Both eyes are painted over. Eye measurements made while the animal was walking

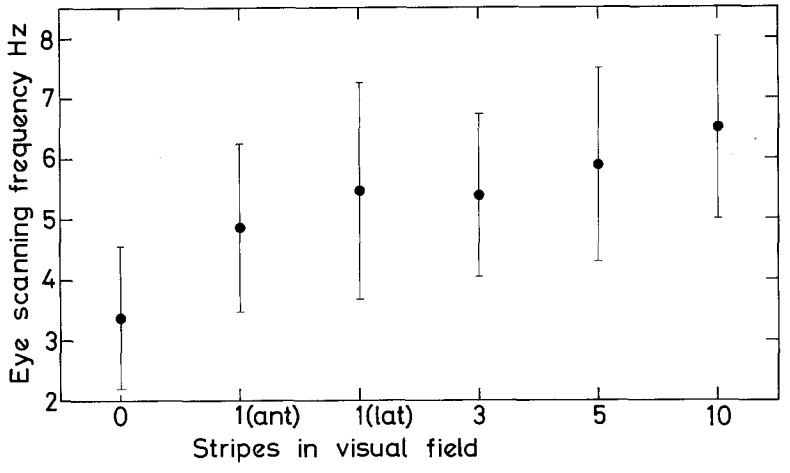

Fig. 6. Frequency of eye scanning with different numbers of stripes in the visual field. Number of cycles averaged: 0=92; 1 stripe anterior=155; 1 stripe (lateral)=201; 3 stripes=178; 5 stripes=241; 6 stripes=357. Bars: S.D.

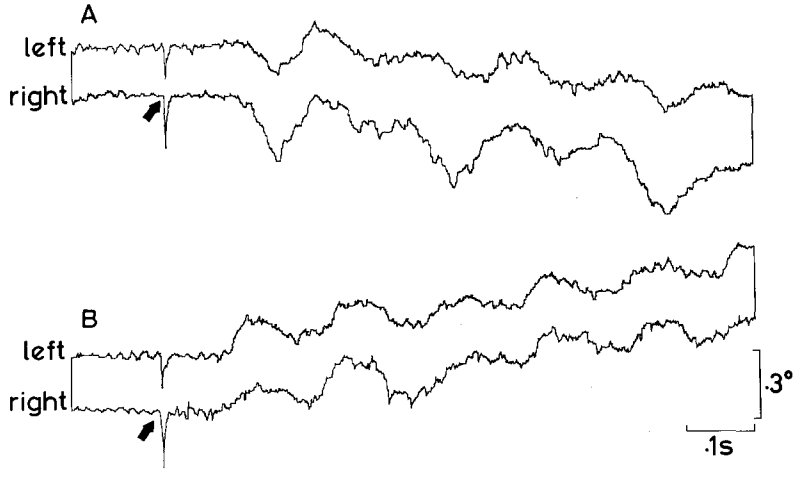

Fig. 7. Latency of optokinetic response to a striped pattern accelerated from a velocity of 0°/s to 0.5°/s. Movement down the page is towards the right, up the page toward the left. Pattern starts to move at arrow

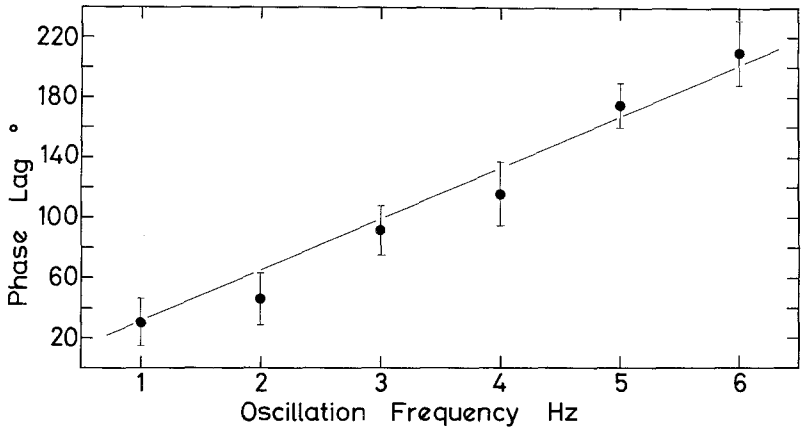

Fig. 8. Increase in phase lag of eye related to a moving striped pattern with increase in frequency of oscillation of pattern. Bars: S.D. Solid line: expected phase lag of a system which has a constant delay of 90 ms built into it

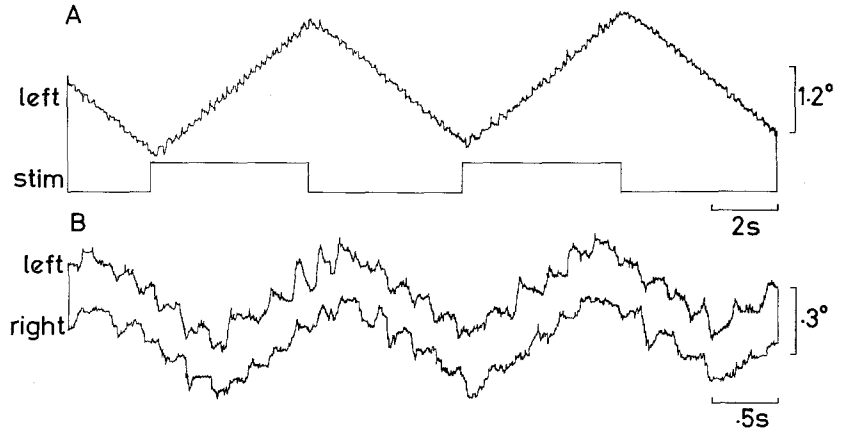

Fig. 9A and B. Eye scanning during smooth tracking of a striped pattern which turned around the animal at 0.5°/s.
A Constant velocity of stimulus against movement of the left eye.
B Responses of both eyes showing scans to be loosely phase coupled

than it (about 6°/s.) After an initial scan which occurred in a space of about half the latency, the eye oscillations continued so that the time taken from the extreme of an excursion in one direction to the extreme in the other direction was very nearly the same as the latency of the initial response (Fig. 7). The actual velocity of the eye during the tracking alternated between 3 and 6°/s. If the stripes were moved back and forth at increased frequency (but at the same velocity) the eyes lagged behind the movement of the stripes and at 5 Hz they were in antiphase with the pattern. This is to be expected of a system with a constant delay of about 90 ms in the feedback loop (Fig. 8).

6. Eye Scanning and Smooth Tracking

Eye scanning during optokinetic movements has been reported to occur in *Carcinus* (Sandeman, 1963) and is also present in *Leptograpsus* (Fig. 9). The scans were of the same frequency and amplitude as those which occurred during walking and did not adapt. The two eyes maintained the same loose phase coupling as in scanning during walking.

Discussion

Whenever the crab *Leptograpsus* walks its eyes scan back and forth and these scanning movements continue as long as the animal moves its legs. The probable mechanism by which the scanning is generated and the functional significance of eye scanning to the animal is discussed here.

1. Generation of the Eye Scanning

Optokinetic eye movements in the crab are controlled by a simple negative feedback loop in which the perception of a difference in the velocity between the visual surround and the retina (the slip) drives the optokinetic system and the eye muscles so that the eye moves to correct this difference in velocity. The eye movements are always conjugate and there are

no proprioceptors monitoring the position of the eyes relative to the body. In this simple servo-system, if the eye is itself displaced in relation to a stationary surround it will move to counteract the displacement (Sandeman, 1963).

Several observations support the conclusion that the mechanism generating eye scanning and the optokinetic system are closely linked. The frequency of eye scanning for example is related to the number of stripes in the visual field, while in the dark or with the eyes blinded there is no scanning. This would seem to rule out the possibility of a central oscillator which was independent of visual feedback. Also, a stripe at the side of the eye produces marginally higher frequencies of scanning than one at the front, and a characteristic of the optokinetic response of *Leptograpsus* is that it is driven more effectively by an input to the side of the eye than one in front (Sandeman, 1978). In addition, at the highest observed frequency of eye scanning the time taken for a change in direction of the eye is about 80 ms which is close to the measured latency for the optokinetic response, and the scanning movements, like the optokinetic movements, are loosely conjugate.

Most of the properties of the eye scanning could therefore be predicted from what is known about the optokinetic system, except that the servo-system of the optokinetic system as described may not on its own be expected to produce a sustained oscillation, and the eye movements during scanning are not sinusoidal but change their direction abruptly at the end of each scan.

To maintain the oscillation in the servo-system requires the injection of another signal which does not need to be at the same frequency as the scanning, but which needs to be large enough to cause the eye to move to one side or the other until the threshold of the corrective visual feedback is crossed. The existence of such a signal which is related to walking has already been described for the crab. It has been noticed that the neural discharges to the eye muscles in a crab were significantly increased in frequency, when the animal was 'aroused'. The arousal was achieved by mechanically stimulating the animal's body and particularly its legs (Wiersma and Fiore, 1971). In a walking crab it could therefore be expected that there is considerably more activity in the motoneurons of the eye muscles than in a resting animal, and this could lead to the initial displacements of the eye which are then counteracted by the visual feedback. The characteristically sudden way in which the correction is achieved, and the hunting which can be seen when the animal is tracking a slow moving striped pattern, are both suggestive of the activation of a relatively high gain system after a certain threshold. Again there is a quite satisfactory explanation for this behavior. The eye muscles of the crab are driven by both tonic and phasic systems (Horridge and Burrows, 1968) and it has been shown that the phasic system has a distinctly higher threshold than the tonic system in the optokinetic response (Sandeman et al., 1968). The sudden change in the direction of the eye in scanning is therefore probably brought about by the activation of the phasic system. Additional evidence for the activity of a phasic system comes from recordings of muscle activity in *Carcinus* where it was shown that small tremor movements of the eye are correlated with a phasic discharge in one of the eye muscles (Horridge and Burrows, 1968).

2. *Functional Significance of Eye Scanning*

Of the many possible advantages of eye scanning, two which are often mentioned are the possibility to improve the spatial resolution of a visual system and the overcoming of adaptation to images which are stabilized on the retina.

Spatial resolution in the compound eye can be limited by diffraction in the dioptric apparatus, by the angular separation between the receptors and by the noise in the receptor apparatus (Kirschfeld, 1976; Snyder et al., 1977). It is possible to calculate the limit of resolution imposed by the dioptric apparatus knowing the wavelength of light passing through it and its aperture, and thus to estimate if effectively decreasing the angle between the receptors by scanning the eye will achieve a greater spatial resolution (Kirschfeld, 1976). In the crab the facet diameter around the equator of the eye is such that an angular separation between the receptors of less than 0.3° would not achieve a greater spatial resolution because the eye would then be diffraction limited. The angular separation between the ommatidia around the equator of the eye of *Leptograpsus* is about 1.5° (Sandeman, 1978) and so, theoretically, temporal scanning could improve the spatial resolution, provided that it is not already limited by noise in the receptors. A satisfactory test of this depends upon presenting *stationary* patterns to the animal and then controlling the relative movements of the eyes. Unfortunately no behavioral test has yet been devised to discover whether a crab has or has not seen a stationary object in its visual surround.

Adaptation of visual systems to images which are stabilised on the retina is known in both vertebrates and invertebrates. In man, stabilized images first lose their contours, then colour and finally brightness

(Gerrits and Vendrik, 1972). Normally this 'fixation blindness' is most likely prevented by continual small, rapid eye movements (Ditchburn and Ginsborg, 1952; Ditchburn and Drysdale, 1977a, b). The fly, *Musca,* will not orient towards a small black spot in its visual field if this is arranged to move with the animal (Reichardt and Poggio, 1976). Significantly, however, if the intensity of a target is flickered, the fly will orient towards it in spite of there being no movement of the target relative to the retina (Pick, 1974).

There is no behavioral evidence for fixation blindness in the crab, and that adaptation in the visual system occurs can only be inferred from electrophysiological recordings from second and higher order neurons in the optic lobe. Lamina cells from which recordings have been made, adapt rapidly to changes in light intensity and do not carry a continual representation of the intensity level of the light falling on the receptors connected to them (Erber and Sandeman, 1976). It may be that there are other types of lamina cells which do not adapt so rapidly, but these have not yet been found. Also, the axon from one retinula cell in each ommatidium extends through the lamina and down into the external medulla (Stowe et al., 1977) and this could relay the level of light intensity at the periphery to the deeper levels of the optic lobe. Higher order neurons do have longer time constants but again adapt after 10 to 15 s (Erber and Sandeman, 1976).

The angular acceptance of retinula cells in *Leptograpsus* eye is about 2° in the dark adapted day-eye (Leggett, 1977) and a 0.5° displacement of a 1.8° light spot can cause a change in the potential of the retinula cells of between 2 to 6 mV if the spot is aligned just off-axis (Sandeman and Hardie, unpublished). Eye scans in the crab are therefore large enough to produce significant fluctuations in the retinula cell receptor potentials. The coupling between the retinula cells and at least one type of lamina cell in the crab is virtually A.C., and there is evidence that the amplification of the signal between the retinula cells and the lamina cells, which occurs in the dragon fly (Laughlin, 1973), also occurs in the crab, because the lamina cells saturate at light intensities which are less than those required to saturate the retinula cells (Erber and Sandeman, 1976). Thus eye scanning in the crab, by modulating the signal which occurs in the retinula cells, will ensure that the signal is passed across the retinula-lamina cell synapse. It is tempting to propose that the real function of the eye scanning lies here, and that the crab is using the familiar electronic principle of a chopper amplifier.

3. Scanning in Other Invertebrates

Side to side movements of the eyes, heads and bodies are now known to occur in a number of animals. The crab *Pachygrapsus* will oscillate its eyes back and forth at the same amplitude and frequency as *Leptograpsus* although in *Pachygrapsus* the eye movements are more regular and can be evoked by simply changing the intensity of the ambient light (Sandeman, unpublished). Jumping spiders will fixate on an object in the field of view of their large frontal eyes and scan it as long as the object is fixated (Land, 1969). *Copilia,* a pelagic copepod, scans its eyes back and forth at a frequency of 5 Hz (Gregory et al., 1964) and in several species of flies a small and special muscle which is attached to the anterior edge of the retina is probably responsible for the continual movements of the deep pseudopupil (Hengstenberg, 1971; Franceschini and Kirschfeld, 1971; Patterson, 1973). Larger, side to side movements are seen in bees which hover in front of flowers, and mantids and locust hoppers which peer. In the locust hopper, the peering has been shown to be correlated with distance perception (Wallace, 1959), but the functional significance of many of these movements, which are so obvious in unrestrained animals, has not been fully explored. An attempt to understand the intricacies of the visual system, certainly at the level of the higher order neurons, has to take into account the fact that during most of the animals life, visual signals are continually modulated in intensity by the animals own movements and the world is rarely presented to the visual system as a stationary array of intensities.

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