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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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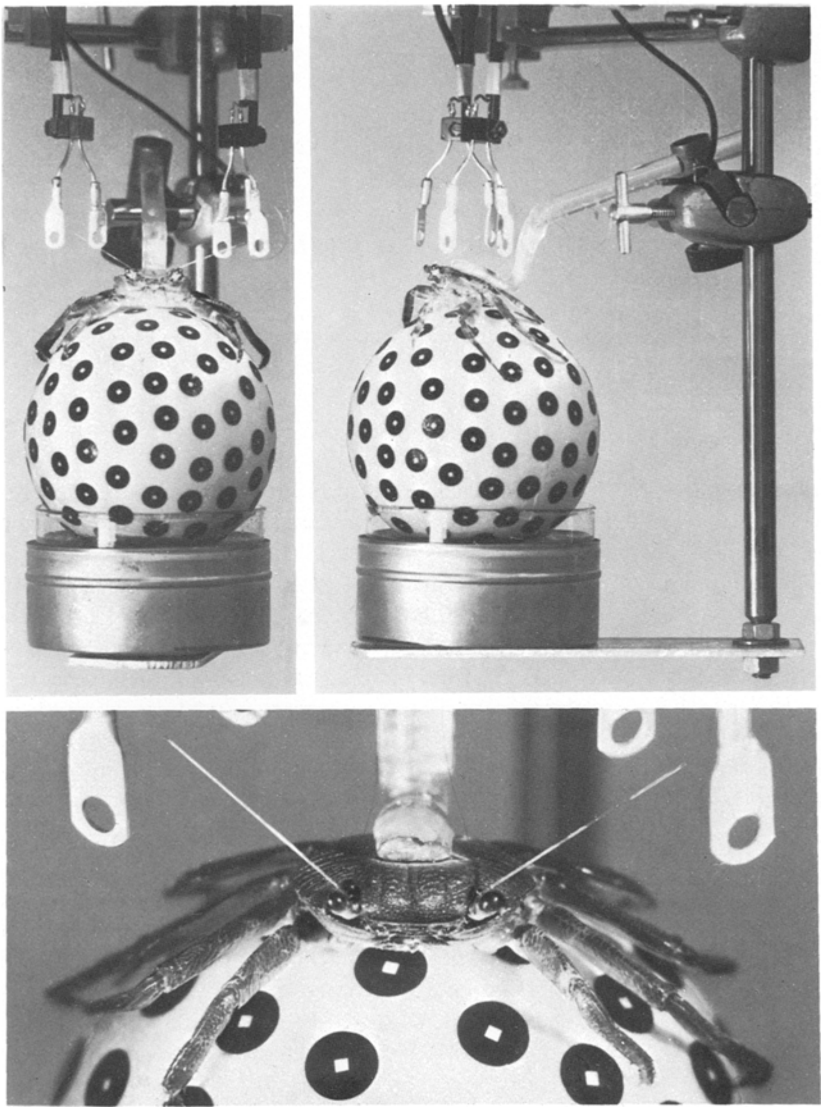

Fig. 1. Experimental set-up used to measure eye movements of the crab walking on a polystyrene ball, seen from front and from side. Animal glued by its back to the perspex rod. Polystyrene ball partially supported by water in the glass bowl beneath it. Lower picture shows the glass fibres on eyes of 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