DISCRIMINATION BETWEEN MOVEMENTS OF EYE AND OBJECT BY VISUAL INTERNEURONES OF CRICKETS

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INTRODUCTION

Every animal faces the problem of distinguishing shifts of the light distribution on its retina which are caused by the movement of objects in the external world from those which are caused by movement of the eye itself. This is an example of a general distinction, which von Holst & Mittelstaedt (1950) have emphasized, between sensory inflow resulting from events occurring independently of the animal (Exafferenz) and that occurring as a direct result of behaviour (Reafferenz).

The present study explores the discrimination between self- and object-movement in terms of the responses of a single pair of visual interneurones in the ventral nerve cord of crickets. The basic observation, that these neurones follow hand movements with a vigorous discharge but are silent when the animal moves its head, is similar to descriptions given by Wiersma & Yamaguchi (1967) for some crayfish visual neurones which become unreactive when the eye moves on its stalk. The cricket neurones, however, have an important advantage for experimentation in that they can be identified physiologically in almost every preparation on the basis of spike size and functional properties. Furthermore, they can be studied as a matched bilateral pair. This paper is devoted primarily to qualitative experiments which demonstrate the operation of an inhibitory mechanism in self-movement vs. object-movement discrimination.

MATERIAL AND METHODS

Adult house crickets (Acheta domesticus), purchased commercially as adults or raised in the laboratory from late instar juveniles, were used in all experiments. Females were preferred for their larger size.

The following method of preparing the animals gave the most consistent results: An adult 1–3 weeks old was induced to autotomize its hind legs and was then anaesthetized with carbon dioxide. A drop of acrylic dental cement was applied so as to hold the head rigidly to the thoracic shield. The animal was then mounted ventral side up on the apparatus, if necessary one eye and the ocelli were painted with a heavy, fast-drying lacquer, and at least 1 hr. was allowed for recovery. The ventral nerve cord was exposed from the ventral side, and the desired connective was lifted on a fine silver wire hook and surrounded by petroleum jelly expressed from a syringe. The second electrode was inserted into the abdomen. Animals prepared in this way lived for several days, but recording conditions usually deteriorated after 4–5 hr.
Controlled movements of the preparation were obtained from a modified Sanborn pen-writer galvanometer driven by a DC power amplifier (Fig. 1). The appropriate waveforms were obtained from a Wavetek function generator and other special sources. For experiments requiring a controlled visual field, a plastic cylinder sprayed with extremely flat black paint (3M brand ‘Velvet Coating’) was mounted concentric with the shaft. At the front of the apparatus, centred over the cricket's head, was a removable white transluscent hemisphere (one half of a table-tennis ball) held in place by a retaining ring. Stationary patterns were made on these hemispheres from strips of black vinyl tape. Moving stimuli were obtained from suitable cardboard vanes mounted on a loudspeaker cone, positioned in place of the slide in a 35 mm. projector, and focused directly on the surface of the hemisphere.

Crickets appear to be very sensitive to heat. For this reason, wax was avoided in mounting the preparation, and all lights were heat-filtered. The fibres under study respond best to novel stimuli, and 30 sec. intervals between trials were required to maintain a constant level of response. The ability to maintain good recording conditions for several hours was therefore essential.

RESULTS

Object movement vs. eye movement

It is easy to elicit a long train of impulses from these large fibres, henceforth called the A fibres, simply by moving one's hand or walking around the room (Fig. 2A). If, however, one records while observing an animal whose head has not been rigidly fixed, it quickly becomes apparent that head movements are not accompanied by any impulses.

A more controlled demonstration of this last property is shown in Fig. 2B, an example of the response of an animal prepared in the following way: The opposite eye and all three ocelli were covered with black lacquer; the antennae were cut off at the base of the flagellum; the ventral nerve cord was completely transected posterior to the cervical recording site; and finally, the whole animal—head, thorax and abdomen—was fixed rigidly to the shaft of the galvanometer. The one remaining eye
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viewed the normally illuminated laboratory. Rotation through $30^\circ$ at a rate comparable to the slow hand movement of Fig. 2A elicited no spikes whatsoever.

This simple experiment both demonstrates the phenomenon under study, and excludes a number of possible physiological explanations.

(1) The movement was imposed and not voluntary, so a centrally generated compensatory or inhibitory mechanism, such as the von Holst ‘Efferenzkopie’, cannot be necessary, though it could be an additional factor operating during voluntary movement.

(2) The mechanism is not dependent on synchronous input from the other eye or the ocelli.

(3) It cannot depend on specific mechanoreceptors in the neck, such as the conspicuous bristles on the front margin of the thoracic shield or subcuticular sense organs. Since the connectives were cut, it cannot require more generalized mechanical stimulation accompanying movement, such as the bending of cercal hairs, unless the mechanosensitive organs are on the head.

I conclude that the sense organ which produces this discrimination is in fact the eye supplying the A fibre under study, and evidence that the expression of this property is governed by the nature of the visual input accompanying eye movement is presented below.

Receptive field

In order to design more analytical experiments, it is necessary to know the geometry of the receptive field of the A fibres. The map shown in Fig. 3 was obtained by positioning a diffuse light source, about $1^\circ$ in diameter at the eye, by means of a perimeter, and plotting the average responses to five consecutive one-second off-pulses. Several features are apparent:

(1) The receptive field is very large—the map shows it extending $160^\circ$ dorso-ventrally and mediolaterally, and it is possible that the dorsal and posterior margins were unfairly restricted by the apparatus used to mount the animal.

(2) The centre of the field is clearly more responsive than the margins, but this centre itself is about $80^\circ$ in diameter, vastly larger than the total fields of neurons familiar in vertebrate visual systems.

(3) The field, including its most responsive central area, extends well to the opposite side of the mid line. There is a large anterior sector of about $100^\circ$ which is viewed
binocularly. Substantial overlap of receptive fields is compatible with the observation that the large pseudopupils of both eyes are seen simultaneously when viewing the eyes from the front or the top.

**Rate of eye movement**

The possibility that simply the rate of movement of the eye against the world might determine the magnitude of the A fibres' response can be tested and eliminated by mounting an animal as described above and letting the galvanometer shaft rotate through the same arc but at different speeds. The results for three animals are shown in Fig. 4. If the total number of spikes is the criterion of response used and their spacing in time ignored, the rate of movement (in a range from below to well above the casual hand movement of Fig. 2A) is of no significance.

One other general point is apparent from Fig. 4. The level of response—the actual number of spikes occurring in response to a given stimulus—is rather different in different individuals. Yet, the effect of altering a stimulus parameter is highly reproducible in healthy preparations.
**Complexity of the visual field**

Why, then, does a moving object of moderate size excite, while relative motion between the eye and the whole world does not? The A fibres might require something which is lacking in the latter stimulus, for example, relative movement of contrasting objects in the world. Alternatively, the stationary world might be a qualitatively adequate stimulus, and the potential response of the fibre be prevented by some inhibitory mechanism. This section demonstrates that, in fact, a stationary but simplified visual world does excite when the eye is moved passively, while a complex one does not. The next section demonstrates that a complex world does inhibit, while a simple one does not.

![Graph](image_url)

Fig. 4. Response to rotation at different rates. The average number of spikes in five to ten consecutive trials is plotted for each of three animals against the rate at which a 30° rotation was imposed on the animal.

A normally illuminated laboratory constitutes a highly complex visual environment, and demonstrates well the resistance of the A fibres to response during forced eye movement (Fig. 4). But in order to clarify the influence of complexity on these fibres, it is necessary to control the structure of the visual field. A reasonably homogeneous environment was obtained by mounting the cricket behind a table-tennis ball as described under Methods. Structure was added to this field by applying strips of black tape, subtending about 8° at the eye, to the outside of the hemisphere in various patterns. These are illustrated under the abscissa of Fig. 5, which shows on the ordinate the results of moving the eye past fields of varying complexity. The response is greatest when the eye rotates past simple patterns; with complex patterns it falls to the level obtained under the most homogeneous conditions available. The response to these particular patterns is never great, but the influence of the degree of complexity is, nevertheless, clearly evident.
Direct demonstration of inhibition

A moving shadow projected on to the white hemisphere facing the cricket (Fig. 1) is a very potent stimulus. Trains of impulses lasting several hundred milliseconds, at an average frequency of 100 per second, can often be obtained. This powerful response can be reduced almost to zero by forced eye movement in a complex visual field, but not in a simple one.

The sequence of events in this rather complex experiment was as follows: (1) start shadow movement, (2) start eye movement, (3) stop eye movement, (4) stop shadow movement; the time relationships are indicated by the long (shadow movement) and short (eye movement) black bars in the graphs of Fig. 6. The response is presented in the form of a latency histogram—the time from the onset of shadow movement was divided into 20 msec. intervals, and the number of spikes occurring in each interval was counted and averaged for five presentations of the stimulus sequence. The dashed line in each graph shows the control response, i.e. the latency histogram of the fibre's response to shadow movement alone. The solid line shows the effect of superimposing eye movement on shadow movement, the pattern against which the eye moved being indicated by the inset figure.

The control histograms obtained for the four conditions of Fig. 6 are all rather similar, both in peak value and in time course. In the absence of eye movement, a
stationary background does not influence the response to a moving shadow, which is consistent with the fact that hand movement against a complex world is an excellent stimulus.

When a rapid rotation of the eye (15° excursion at 300°/sec.) was superimposed on the shadow stimulus, the inhibitory effect of the complex background was clearly revealed (Fig. 6A, solid line). The response during eye movement was severely depressed, and remained so for the duration of the shadow movement. A simpler background (Fig. 6B) or a smaller movement (Fig. 6D) produced less powerful and less prolonged inhibition, and in the latter case the cessation of eye movement was followed by a post-inhibitory rebound.

Figure 6C shows that a slight inhibition resulted from eye movement even in the absence of a stationary pattern in the visual field. Since in this experiment the excitatory stimulus was a large moving shadow visible to the eye during the eye’s movement,
a truly homogeneous visual field could not be achieved. This is presumed to be the origin of the observed inhibition. The relative inhibitory effectiveness of various patterns is summarized in Fig. 7.

Since the control values in Fig. 6 did not change significantly with the complexity of the background, I conclude that a complex visual world is not itself inhibitory. Since simplification of the visual field produced a marked reduction in the observed inhibition, I conclude that eye movement itself is likewise not inhibitory. But movement of the eye against a complex field will clearly inhibit the response of the A fibres even to an extremely potent stimulus.

Fig. 7. Suppression of response to moving shadow as a function of visual field complexity. Data from the experiment of Fig. 6 are here plotted as a percentage: (total response with movement/total control response) x 100. The closed circles represent 15° rotations, the single open circle a 5° rotation.

DISCUSSION

The experimental results presented above can be reviewed in the following way: In each connective of the cervical and thoracic ventral nerve cord of the cricket runs a large fibre responsive to the movement of objects anywhere in the visual field of the ipsilateral compound eye. It fails to respond when this eye is moved in relation to the world, either voluntarily or forcibly. One mechanism which prevents a response to self-movement is an inhibition which is dependent on the visual stimulus provided by the movement of the eye past a structured environment, and which disappears when the eye is moved against a homogeneous environment. In the terms of von Holst & Mittlestaedt (1950), the fibre responds readily to Exafferenz, but its connections with the retina are such as to prevent a response to visual Reafferenz under plausible natural circumstances.

Fibres in the ventral nerve cord of locusts which are closely analogous to the cricket
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A fibres were described previously in terms of stationary stimuli (Palka, 1967a). An argument was there presented for the existence of an inhibitory system with inputs identical with or at least intermingled with the excitatory inputs which converge from the whole eye on to each ventral cord cell. The inhibitory component was emphasized by increasing the area of a dimming stimulus—increasing the number of ommatidia simultaneously activated. This is also accomplished by increasing the complexity of the field against which the eye sweeps during head movement. Since the locust fibres also ignore head movement (Palka, 1967b), a common mechanism may well be involved. This would incidentally provide a teleology for cells with very large receptive fields: A moving object anywhere in the field of view of the eye will excite, but eye movement itself will not.

Neurones with large receptive fields, often covering the whole eye, appear to be common among arthropods. This is true, for example, of a variety of cells (both brightness and motion detectors) in locust optic lobes (Horridge, Scholes, Shaw & Tunstall, 1965) and in crustacean optic nerves (Wiersma, 1967); both directional and non-directional motion detectors in the fly (Bishop & Keehn, 1967; Bishop, Keehn & McCann, 1968); and directional motion detectors in the moth (Collett & Blest, 1966). It seems likely that many of these have topographically intermingled excitatory and inhibitory inputs, rather than the regional differentiation so conspicuous in vertebrate retinal (Kuffler, 1953) and cortical (Hubel & Wiesel, 1962) cells.

The most extensive series of observations on arthropod visual systems is that of Wiersma and his collaborators. Among the units studied by Wiersma & Yamaguchi (1967) in crayfish, examples can be found in which a number of the properties demonstrated here for the cricket A fibres are present. In particular, their 'jittery movement' fibres are dimming and movement-sensitive and ignore movements of the eye.

Wiersma & Yamaguchi observed insensitivity to eye movements which were caused by accidental stimulation of motor axons, as well as by manually pushing the eyestalks. They remark that the mechanism in the two cases might be identical, since pushing on the eyestalk could have caused reflex motor activity, in either case resulting in mechano-receptive feedback which inhibited the visual neurones. The principal conclusion reached on the basis of the present experiments is that the inhibitory effect of forced eye movement on cricket A fibres is not dependent on any obvious mechano-receptors or reflexes, but is dependent on complex stimulation of the eye in which each fibre originates. This is reminiscent of the finding of Horridge & Sandeman (1964) that eyestalk movement in crab optokinetic nystagmus is controlled by visual, not mechanosensory input.

Wiersma & Yamaguchi observed that an 'excited state', a presumed widespread alteration in the state of the central nervous system, could influence the response of their 'sustaining fibres', but they could not show the same for the movement fibres. The A fibres described here also appear to be subject to central control, as indicated by the finding that the responses of both members of the pair, originating in two different eyes, fluctuate together under stimulus conditions in which the average response is constant. It is common to observe that when the mouthparts, especially the palps, are active the A fibres are suppressed. Dambach (personal communication) found in the cricket Gryllus campestris that apparently identical visual neurones were silent during voluntary movement in unrestrained animals. These observations
suggest that it may be possible to study here the operation of a central mechanism which adjusts the excitability of visual interneurones in anticipation of the visual consequences of the animal's behaviour.

SUMMARY

1. One large neurone on each side of the cervical and thoracic ventral nerve cord of crickets responds to object motion anywhere in the visual field of the ipsilateral compound eye, but not to the forced or voluntary movement of the eye itself.

2. This discrimination between self-movement and object-movement is accomplished by an inhibitory mechanism mediated by the same eye.

3. Inhibition must be present because a potent moving stimulus becomes ineffective if presented during a forced eye movement.

4. Its visual origin is demonstrated in two ways: (a) abolishing all known mechanosensory feedback does not disrupt the mechanism, but (b) alteration of visual conditions does so in a predictable way. Sweeping the eye past a complex visual environment suppresses the neurone's response to a concurrently or subsequently presented moving target, whereas the same movement past a simplified or homogeneous environment produces little or no inhibition.

5. Responses to eye movement itself are greatly enhanced in appropriately simplified visual fields, reinforcing the conclusion that the inhibition preventing response in complex fields is of visual origin.

6. Suggestive evidence for an additional inhibitory mechanism associated with voluntary movement is presented.

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