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STATOCYST-INDUCED EYE MOVEMENTS IN THE CRAB *SCYLLA SERRATA**

II. THE RESPONSES OF THE EYE MUSCLES

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INTRODUCTION

Crabs are sensitive to angular acceleration. This is demonstrated, in the absence of other stimuli, when blind legless crabs are placed on a turntable and rotated. The eyes are partially stabilized by a slow movement in the direction of the imposed rotation followed by a fast recovery phase in the same direction as the rotation (Dijkgraaf, 1955, 1956).

These nystagmus movements persist only during acceleration, and are in every way like those of most vertebrates subjected to rotational stimuli. In crabs the statocysts have been known for some time to be the organ primarily responsible for the detection of rotational and positional stimuli (Delage, 1887; Kreidl, 1893; Bethe, 1897, 1898; Prentiss, 1901; Fröhlich, 1904; v. Buddenbrock, 1914; Kühn, 1914) and the canal-like organization of these organs with their appropriately positioned sense organs has led to the suggestion that the principle underlying their operation is very similar to the vertebrate non-acoustic labyrinth (Sandeman & Okajima, 1972).

The electro-physiological responses of the different groups of receptors in the statocyst are described in the first paper of this series and in the present paper we compare the responses of eye muscles of intact crabs subjected to rotational and optokinetic stimuli, and relate these with the eye-muscle responses produced by the direct stimulation of the hair receptors in the statocysts of semi-isolated and perfused brain preparations. Two eye-muscle blocks which have particular relevance to rotational studies are muscles 20a and 21 (numbering of Cochrane, 1935) because these muscles are known to be the prime movers for horizontal eye movements in *Carcinus*.

During optokinetic nystagmus the activity in these muscles can be correlated with the position of the eye in the horizontal plane and with the fast and slow phases of nystagmus but is unaffected by tilting about the transverse axis. For example, the frequency of discharges in muscle 20a of the right eye gradually increases during a slow-phase movement to the right while that in muscle 20a of the left eye decreases. During a fast-phase movement to the left there is a burst of activity in muscle 20a of the left eye and inhibition of activity in muscle 20a of the right eye. Muscles 21 and 20a of the same eye are antagonists. (For a summary of the action of all the crab eye muscles see Burrows and Horridge, 1968*a*.)

* This paper is dedicated to Professor Haruo Kinosita on the occasion of his sixtieth birthday.

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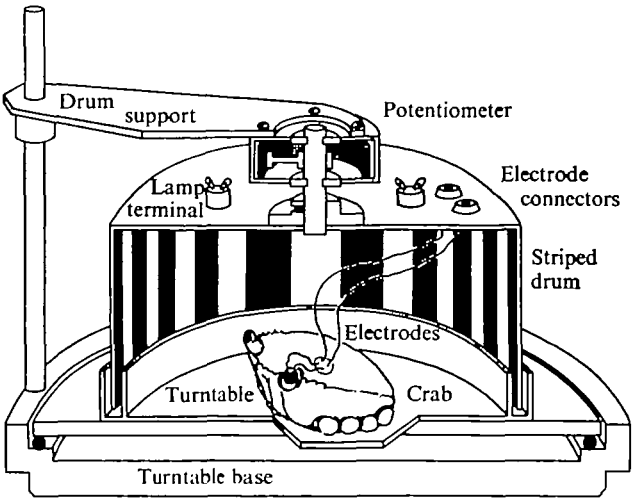

Fig. 1. The apparatus used to produce rotational and optokinetic nystagmus in crabs while recording the activity of selected eye muscles. The crab can be rotated in the dark or light and the surroundings can remain stationary or fixed relative to the crab. For optokinetic nystagmus the turntable remains stationary while the surround is illuminated and rotated. The drum and turntable are rotated by hand and their movements are monitored by the potentiometer and a voltage source.

We have found that as the eye moves under the influence of the dynamic receptors of the statocyst, horizontal eye movements are controlled in the same way as above. Moreover in the isolated eye–brain preparations both the slow and fast phases of nystagmus are generated by direct irrigation of the horizontal canals of the statocyst. We have also been able to confirm that the thread hairs are the statocyst receptors predominantly associated with the nystagmus eye movements.

MATERIALS AND METHODS

Specimens of *Scylla serrata* were shipped from Queensland and kept alive in the laboratory in wet hessian.

For studies on animals with the head region intact the crabs were first forced to autotomize their limbs and were immediately placed on a turntable. Diamel-coated silver wires were passed through small holes in the eye-cup and into the eye muscles. The wire leads were looped and waxed to the back of the animal and then attached to connectors in a metal cover which was positioned over the animal (Fig. 1). Black and white stripes subtending an angle of 7·5° at the eye were painted on the inside of the cover, which could be rotated separately from the turntable or together with it. The animal was in complete darkness with the cover in position but the stripes could be illuminated by lamps inside the cover. The rotation of the cover alone or the cover and the turntable together was monitored by a potentiometer on which the cover was mounted (Fig. 1).

Eye movements were not monitored but the correspondence between optokinetic eye movements and muscle responses could be confirmed by raising the cover and observing the eye while listening to an audio monitor of the muscle responses. Also,

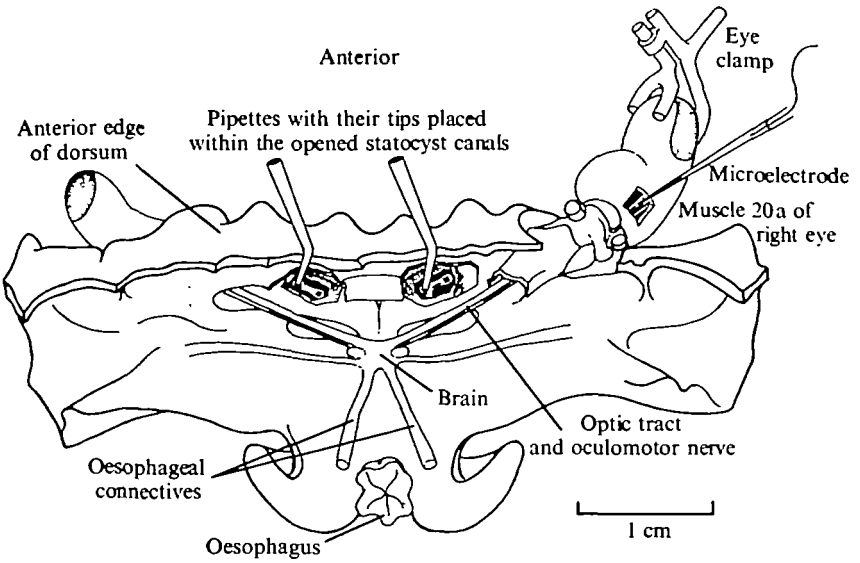

Fig. 2. The isolated eye–brain preparation viewed from behind. The anterior part of the crab (shown here) is cut away from the cephalo-thorax and the statocysts are exposed by removing the proximal portion of the eyestalks. The right eye is extended and clamped and muscle 20a is exposed to allow the insertion of the electrode. Stimulus pipettes are placed in holes cut into the statocyst horizontal canals and the fluid in the canals is allowed to escape through a second set of holes cut at the opposite end of the canals. The brain is perfused through a cannula in the cerebral artery (not shown).

the relationship between eye-muscle discharges and eye movements in crabs is well known from work on *Carcinus* (Burrows & Horridge, 1968*a*, *b*).

Isolated eye–brain preparations were made as described previously (Sandeman, 1971) except that the eye-cup was clamped and extended so that a micro-electrode (10–40 MΩ; 3 M-KCl filled) could be inserted into the eye muscles after part of the eye-cup exoskeleton had been removed. The statocysts on both sides were exposed by cutting away part of the eyestalk without damaging the oculomotor nerves (Fig. 2).

The initial acceleration caused by imposing a rotation about the axis of any fluid-filled circular canal results in a transient flow of fluid through the canals and, in the case of the statocyst canals, a resultant deflexion of the sensory thread hairs. In the isolated crab–brain preparation rotation of the animal was simulated by producing small controlled displacements of the statocyst fluid. This was achieved in the following way. The horizontal statocyst canals were opened in two places, medially and laterally, and the tips of saline-filled pipettes of about 200 μm inside diameter were inserted into the horizontal statocyst canals (Fig. 2). The pipettes were coupled to lengths of rubber tubing also filled with saline and closed at one end. A solenoid-operated clamp pinched the rubber tubing and a small pulse of saline was ejected from the pipette and into the statocyst canal. Power was maintained through the solenoid with a latch relay system and reverse flow of fluid through the statocyst was achieved simply by releasing the clamp which allowed the rubber tubing to resume its initial shape and suck saline back into the pipette.

A micrometer slide on the clamp (Fig. 3) controlled the amplitude of the pinch and

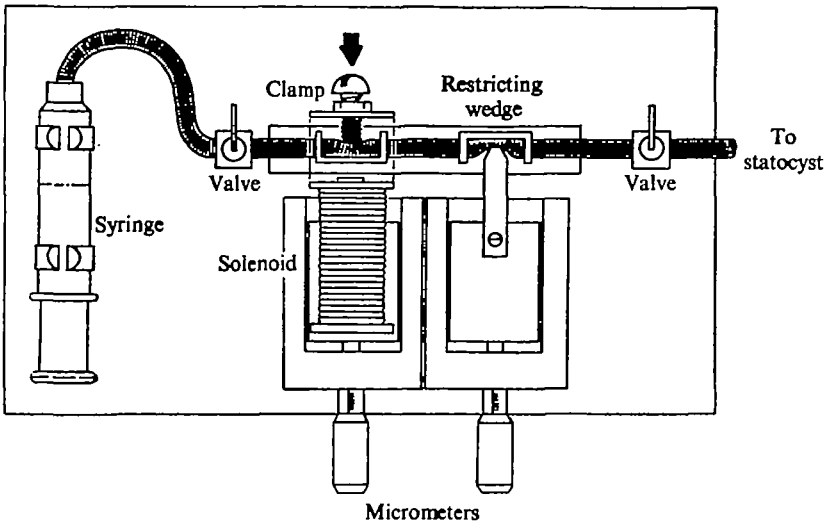

Fig. 3. The statocyst stimulator. Displacement of the fluid in the horizontal canal of the statocyst is produced when the solenoid closes on the rubber tubing which is filled with saline and attached to a pipette inserted into the statocyst. The amplitude of the fluid displacement is adjusted by a micrometer on the solenoid clamp, and the duration of the fluid flow by a wedge which constricts the tubing between the clamp and the statocyst. The syringe is used to fill the system and expel any air bubbles. Each statocyst has a separate stimulator.

thus the amount of fluid displaced. In addition, the flow of saline from the pinched tube to the statocyst canal was restricted by a micrometer-adjustable pinch-cock so that the stimulus duration could be controlled. The onset of the stimulus was electrically monitored but as there is no way of accurately determining the rate of fluid flow within the canals, the duration and amplitude of the stimulus were inferred from micrometer settings. These were calibrated by direct observation of the displacement of a small bubble introduced into the stimulus pipette. Optimal stimuli for each preparation were obtained experimentally. A separate stimulator was linked to each statocyst to allow unilateral and bilateral stimulation.

Electrical responses from the muscles were conventionally amplified and displayed.

RESULTS

Extracellular responses from eye muscles of intact crabs

The anatomical organization of the eye muscles in *Scylla* is very similar to that of *Carcinus* and the electrical responses from the eye muscles of the two crabs are apparently identical.

Extracellular recordings from muscle 20a show that during a slow-phase optokinetic movement away from the midline activity in the muscle gradually increases to a maximum and then is inhibited for a short period at the onset of the fast return phase (Fig. 4*a*). Slow-phase optokinetic movements towards the midline are generally accompanied by a cessation of tonic activity in the muscle. A burst of activity occurs during the fast-phase movement away from the midline (Fig. 4*b*).

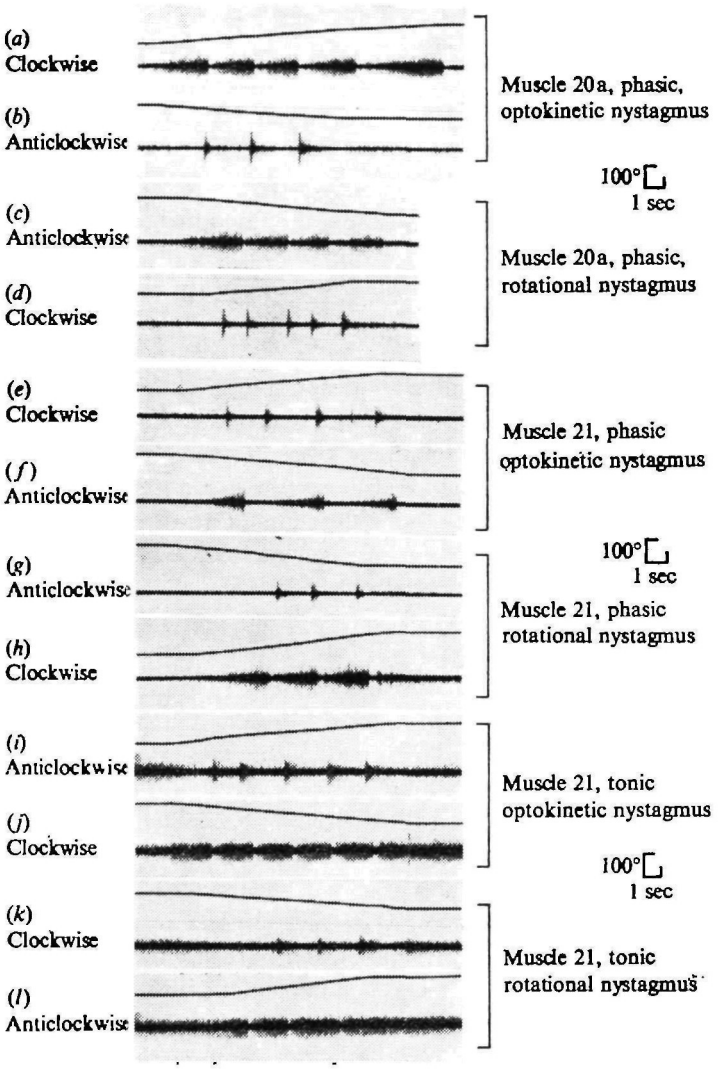

Fig. 4. A comparison of the extracellular activity in muscles 20a and 21 of the right eye during optokinetic nystagmus (*a*, *b*, *e*, *f*, *i*, *j*) with that produced in the same muscles during rotational nystagmus (*c*, *d*, *g*, *h*, *k*, *l*). Upper traces show the drum or turntable movement, lower traces the muscle potentials. Clockwise rotation of the striped drum (*a*) or an anticlockwise rotation of the crab in the dark (*c*) results in a gradual increase in the activity of muscle 20a as it pulls the eye over to the right, followed by a sudden cessation of activity during a fast-phase movement to the left. Abrupt bursts of activity in this muscle during anticlockwise drum movement, or clockwise rotation of the crab (*b*, *d*), signal fast phases to the right between slow phases to the left. The responses of muscle 21 are opposite to those of muscle 20a of the same eye (*e–l*). The increase in the discharge frequency of the tonic units in muscle 21 during slow phases is not as clear as that in the phasic units. However, during anticlockwise stripe movements, or clockwise rotation of the animal, the tonic units show a clear inhibition between the fast-phase bursts (*j*, *l*).

Tonic and phasic activity in muscle 21, however, increase during slow-phase optokinetic movements *towards* the midline (Fig. 4*f*, *j*) and the activity is inhibited for a short period during the fast phase away from the midline. Fast-phase movements toward the midline are accompanied by a burst of activity (Fig. 4*e*, *i*) interspersed with periods of inhibition. Muscles 20a and 21, then, have exactly opposite actions on the eye-cup. Their action is the same as muscles 20a and 21 in *Carcinus* (Burrows & Horridge, 1968*a*).

Rotation of the crab in complete darkness is sometimes more and sometimes less effective than the optokinetic stimulus in the production of nystagmus. Nevertheless clear slow and fast phases occur and the responses of the muscles are generally the same regardless of the way in which the nystagmus is initiated. Small differences in the intensity of the muscle discharges, particularly during the fast phases, are evident in Fig. 4 (*c*, *d*, *g*, *h*, *k*, *l*) and the inhibition of slow-phase activity at the onset of the fast phase is often less pronounced with rotational nystagmus than in optokinetic nystagmus. Movements of the drum and turntable were produced by hand and therefore the velocities of the input signals varied from one test to another and were not entirely constant within a single test so that some differences in the responses must be expected. Nevertheless the similarity between eye movements produced by a rotational stimulus and an optical one are striking particularly when it is considered that there is a powerful visual feedback loop operating in optokinetic nystagmus whereas no feedback loop is known for rotational nystagmus.

Combination of both the optokinetic and rotational stimuli is achieved by rotating the animal on the turntable inside a stationary illuminated striped drum, and this is usually more effective for the production of nystagmus than either optokinetic or rotational stimuli alone. An approximate measure of this summation can be obtained by counting the number of fast phases generated over a known rotational displacement of the striped drum or turntable (usually about 100°) and plotting these against the angular velocities of drum or turntable (Fig. 5). The points on the graphs are scattered but clearly indicate the similarity between the optokinetic and rotationally evoked responses, and the improved performance when both inputs are used together.

An optokinetic input to a single eye is sufficient to produce good slow and fast phases in both directions in unilaterally blinded *Carcinus* and *Scylla*. However, in *Carcinus* the fast phases are more likely to occur when the seeing eye moves toward the midline during its slow phase than when it moves away from the midline during its slow phase. Also, in normal unblinded animals the fast phase of one eye, again the one moving toward the midline during its slow phase, commences its fast phase 30–80 msec before the other eye. The leading eye is called the governing eye and the other the governed eye (Barnes & Horridge, 1969). Ablation of one statocyst causes an initial cessation of both optokinetic and rotationally induced nystagmus. After a recovery period of up to 3 days nystagmus can be elicited again by either input, although less easily from the statocyst input. We could find no consistent differences in the occurrence of fast phases which could be related to the remaining statocyst or to the direction of imposed rotation; nystagmus in both directions can be produced by the input from one statocyst (Fig. 6). Removal of both statocysts does not affect the eye movements produced by the visual input but the animal is no longer sensitive to rotation.

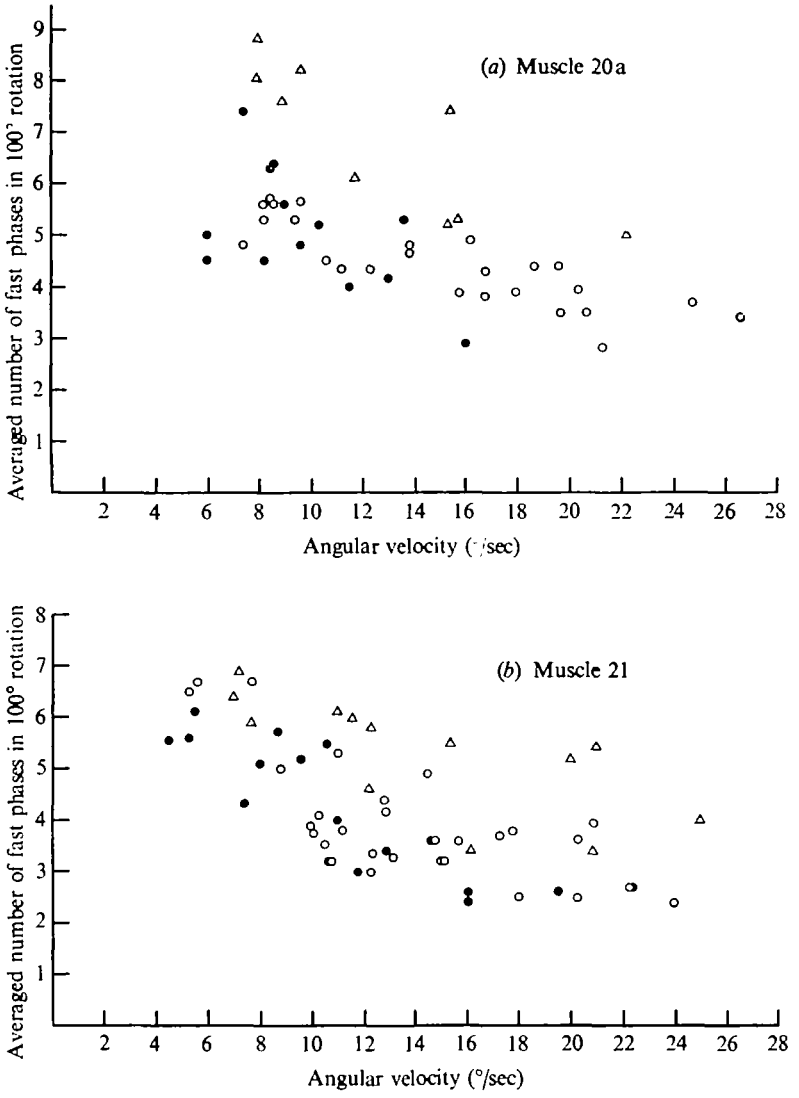

Fig. 5. A comparison of the number of fast phases generated by an optokinetic stimulus (closed circles), a rotational stimulus (open circles) and both together (triangles). The optokinetic and rotational inputs alone appear to be approximately equally effective but together they sum to improve the performance of the system. Both systems show improvement at lower angular velocities although at speeds much slower than those shown the statocyst system will probably not match the visual system so well.

Intracellular responses from the eye muscles of isolated eye–brain preparations

A comparison between the eye-muscle discharges in the isolated preparation produced by direct stimulation of the statocyst with those in the intact animal is necessary to decide whether or not the artificial stimulation is producing nystagmus. In particular it is important that the muscle discharges are appropriate to the direction of fluid movement in the statocyst canals.

When the animal is rotated the fluid in the statocyst canals rotates in the opposite

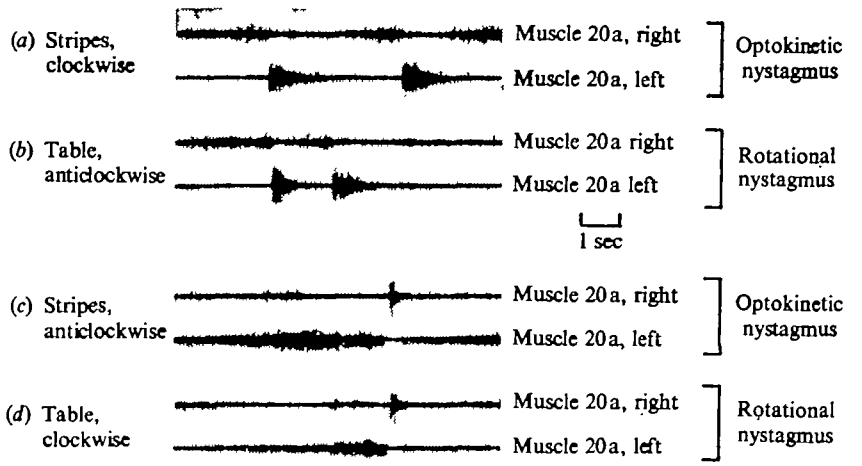

Fig. 6. Optokinetic and rotational nystagmus in an animal with a single statocyst. Extracellular responses are recorded simultaneously from muscles 20a of the right eye (upper trace) and left eye (lower trace). The right statocyst is ablated. The characteristic slow and fast phases are present in both eyes and are initiated by both optokinetic and rotational stimuli. The fast-phase bursts in the muscles of one eye always occur during a period of inhibition of muscle activity in the same muscle of the other eye.

direction. Hence artificial displacement of the fluid in the canals in a clockwise direction is equivalent to anticlockwise rotation of the intact animal and anticlockwise rotation of the intact animal causes the eyes to move slowly to the right. Tonic and phasic activity builds up in muscle 20a of the right eye (and in muscle 21 of the left eye) until a fast phase to the left occurs and the activity in muscle 20a of the right eye is inhibited for a short period (Fig. 4).

In isolated preparations these responses are reproduced in the tonic and phasic muscle units of muscle 20a of the right eye when the fluid is made to flow in a clockwise direction in the horizontal canals of the statocysts (Fig. 7*a–d*). There is an increase in frequency, more obvious in the phasic units, starting immediately after the onset of the stimulus. This is followed some time later by a sudden inhibition of the activity and a resumption of low-frequency firing. The pattern of discharge of these units, besides closely resembling our own extracellular recordings from the intact animals, are exactly like the intracellular responses of the same muscles in the eyes of *Carcinus* during optokinetic nystagmus (Burrows & Horridge, 1968*b*).

Reversal of the stimulus produces inhibition of the ongoing activity in muscle 20a of the right eye followed by one and sometimes two bursts of activity such as that found during the fast phase in the same eye muscle of an intact animal (Figs. 4).

Recordings from muscle 21 of the right eye in isolated preparations show the same kinds of responses except that the slow phases appear during anticlockwise rotation of the statocyst fluid as would be expected (Fig. 7*e, f*). In every case the intracellular responses show that the muscle cells are multiterminally innervated and that all the cells that we recorded from are activated during both slow and fast phases in the same direction. If the thread hairs alone remain intact and all the other statocyst nerves are destroyed, nystagmus responses in the muscles can still be generated.

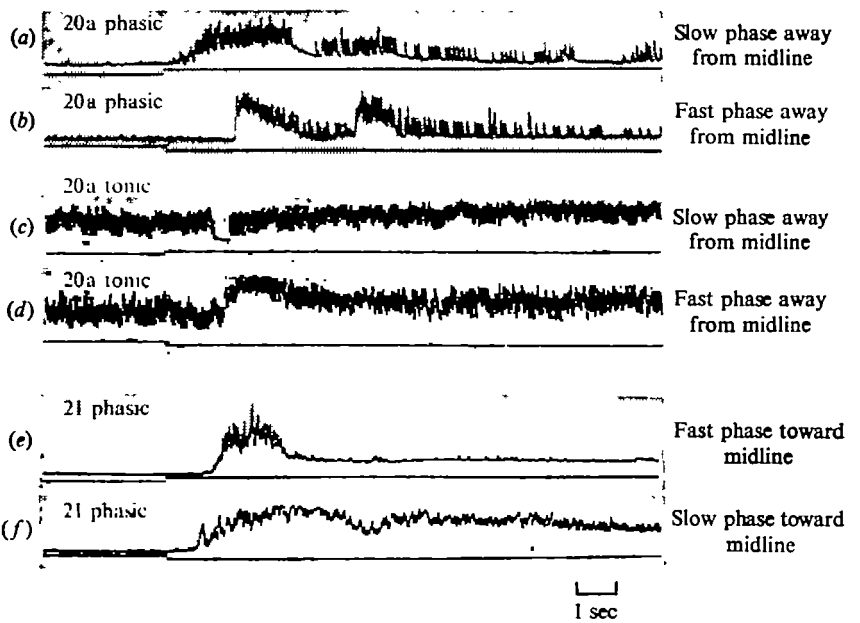

Fig. 7. Intracellular muscle responses from the right eye of an isolated eye–brain preparation, produced by direct irrigation of the statocyst canals. The onset and direction of the stimulus is shown in the lower trace. The recordings show the increase in frequency produced during a slow phase (*a*, *c*, *f*) and fast-phase bursts in the same muscle units produced by changing the direction of the stimulus (*b*, *d*, *e*). Interruptions in the trains of spikes in the slow-phase responses of *a* and *c* are fast phases. Irrigation of the statocyst rarely evokes more than one or two fast phases but slow-phase excitation can always be produced.

The effect of stimulating the statocysts separately

Extirpation of one statocyst from an otherwise intact animal shows that the remaining statocyst provides enough information about rotational stimuli to produce nystagmus in both eyes. However, this experiment does not reveal the interaction, if any, between two operational statocysts.

In the isolated preparation it is a simple matter to stimulate either statocyst separately and watch the effect on the eye muscles. The inputs are not damaged as in the case of intact animal studies, but are just not activated.

A clear summation of the inputs from the two statocysts can be demonstrated by adjusting the intensity of the stimuli to the statocysts one at a time until neither gives a complete response, and then applying the stimuli to both whereupon nystagmus is produced (Fig. 8*a–c*). The summation is obviously occurring before the muscle because the subthreshold inputs often cause little or no response in the muscles at all. Recordings from motoneurones will reveal whether the summation is pre-motoneurone or not.

A slight bias in the responses of the eye muscles to unilateral statocyst stimulation is revealed at low-stimulus intensities. For example, slow-phase activity and inhibition during the fast phases in muscle 20a of the right eye occur when the fluid in both statocysts is made to flow in a clockwise direction. Reversal of the flow produces fast-

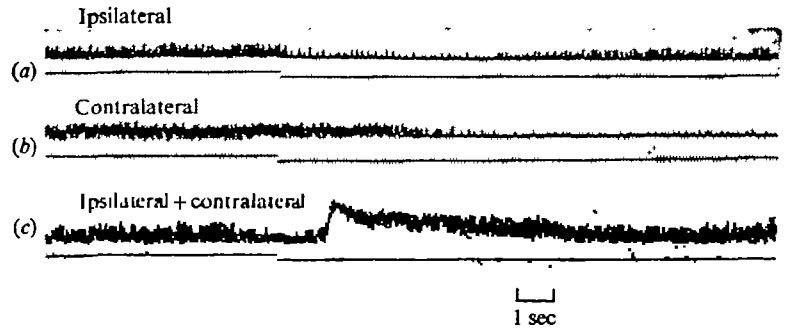

Fig. 8. Summation of the statocyst inputs in the isolated eye–brain preparation. Stimulation of the ipsilateral statocyst at low intensity results in an inhibition of the tonic activity in muscle 20a of the right eye but no fast phase (*a*). Stimulation of the contralateral statocyst has the same effect (*b*). When both statocysts are stimulated simultaneously without altering the individual stimulus intensities, a fast-phase burst is generated indicating a summation of the inputs from the two statocysts.

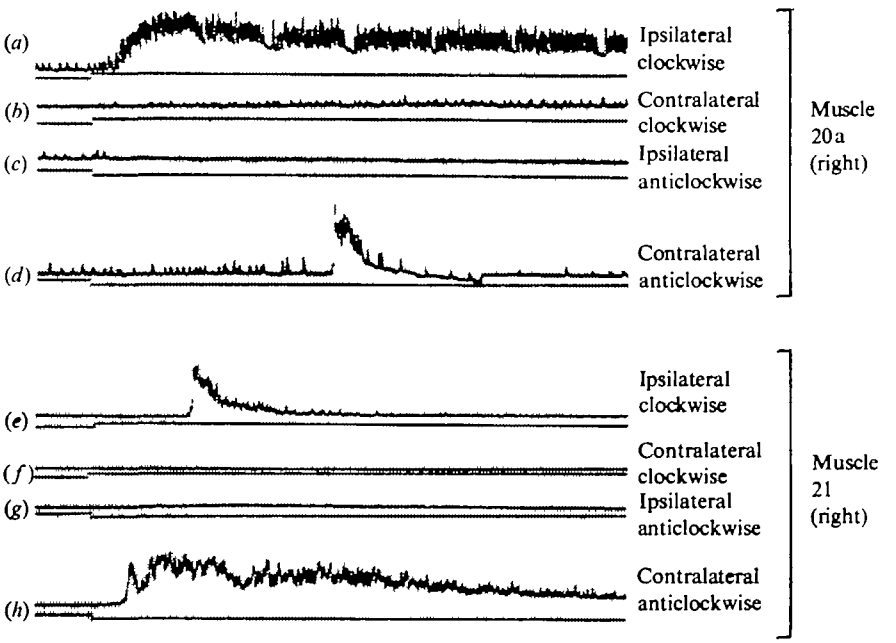

Fig. 9. Intracellular recordings from muscles 20a and 21 of the right eye to show the result of stimulating only the ipsilateral or contralateral statocysts. The greatest response of the muscles is obtained when the fluid is driven clockwise in the ipsilateral statocyst (*a*, *e*) or anticlockwise in the contralateral statocyst (*d*, *h*). Fluid movements opposite to these have little effect on the eye muscles (*b*, *c*, *f*, *g*). The stimulus intensities for *a–d* and *e–h* were kept constant.

phase bursts (Fig. 7*a*, *b*). If the fluid in the ipsilateral statocyst is displaced in a clockwise direction and the contralateral statocyst is not stimulated, a slow phase in muscle 20a of the right eye is still produced (Fig. 9*a*), but when the stimulus is reversed the expected fast-phase bursts do not occur (Fig. 9*c*). Stimulation of the contralateral statocyst produces an opposite effect. Clockwise fluid movements do not produce the

expected slow phase in muscle 20a of the right eye (Fig. 9*b*) but anticlockwise flow evokes a fast-phase burst in this muscle (Fig. 9*d*).

A similar result is obtained for muscle 21 of the right eye where clockwise rotation of the fluid in the ipsilateral statocyst produces good eye-muscle responses but anticlockwise rotation does not. Anticlockwise rotation of the fluid in the contralateral statocyst is a more effective stimulus than clockwise rotation of fluid in this statocyst (Fig. 9*e–h*). Slow-phase eye movements to the right, therefore, are evoked primarily by the right statocyst and to the left by the left statocyst.

The possibility that the bias is inherent in the stimulator can be ruled out because there is no correlation between the application or release of the clamp on the rubber tube and the effectiveness of the stimulus. The position of the stimulating pipettes in relation to the statocyst canals can also be excluded as a cause of bias because the effect is produced regardless of whether the pipette is in the medial or lateral part of the canal.

DISCUSSION

Irrigation of the statocysts as an adequate stimulus

Irrigation of the statocysts in the isolated eye–brain preparation of the crab produces activity in the eye muscles which closely resembles that of intact animals during rotationally induced nystagmus. This can be taken to represent genuine nystagmus for the following reasons. First of all the eye-muscle responses are always appropriate to the direction of the stimulus. Slow-phase activity in muscle 20a of the right eye, for example, occurs in the intact animal when it is rotated anticlockwise and would be expected to occur in the isolated preparation when the statocyst fluid is displaced in a clockwise direction. This result is consistent. Similarly if the direction of rotation is reversed, activity in muscle 20a should be inhibited. This result is also consistently obtained and is significant because it excludes the possibility that direct statocyst stimulation merely raises the general level of excitation in all the muscles of the eye, a phenomenon which does follow the increase in non-specific sensory input to the animal (Wiersma & Fiore, 1971). The second important correlation between the responses of the eye muscles of the intact animal and those of the isolated preparation is the occurrence of fast phases, represented either by a sudden cessation of activity or a burst of activity following an initial inhibition of the ongoing activity of the muscle. Again, fast-phase muscle responses are always appropriate to the direction of the stimulus. Furthermore, the responses of the single muscle cells in the isolated preparation closely resemble those obtained from *Carcinus* during optokinetic nystagmus (Burrows & Horridge, 1968*a*, *b*).

Given that direct stimulation of the statocyst produces nystagmus in the isolated brain preparation, the intracellular responses of the eye muscles can be used to characterize the responses of their motoneurones. This is a necessary step before the investigation can be carried into the central nervous system. The indications are that the motoneurones associated with nystagmus range from tonic to phasic in their discharge patterns. It is also evident that the same motoneurone, as identified by intracellular muscle potentials, may be activated during both the slow and fast phases in the same direction as are the medial rectus motoneurones in the fish (Korn &

Bennett, 1971). Identification of the motoneurones in the brain will depend on their appropriate slow-phase or fast-phase responses to the directional stimulation of the statocyst.

The directional bias of the statocysts

A comparison between the responses produced by bilateral stimulation (Fig. 7) and unilateral stimulation (Fig. 9) shows that for muscles of the right eye the best responses are always obtained when the fluid is rotated in a clockwise direction in the ipsilateral statocyst or anticlockwise in the contralateral statocyst. Put in another way, the right statocyst is dominant when the eyes are driven to the right and the left statocyst is dominant when they are driven to the left. The dominance of the statocysts is obviously not complete because a crab with a single statocyst can produce nystagmus in both directions, and eye-muscle recordings from isolated eye–brain preparations show that the inputs from the separate statocysts are summed within the brain. The bias may be imposed at the statocyst by a preferential sensitivity of the thread-hair receptors to a deflexion in one direction, and although this was not detected in recordings from the receptors (Sandeman & Okajima, 1972) the possibility cannot be completely excluded without recording from every hair.

The nystagmus system in the crab

The advantage of moveable eyes to invertebrates and vertebrates with non-foveal vision does not lie so much in the ability to cover a wide visual field without moving the head as to provide the animal with clear vision during movements of the head and body. This is done by keeping the eyes stationary relative to the environment while the animal turns, and the eye-movement mechanisms to achieve this have been evolved separately in both groups of animals but have remarkable similarities. The nystagmus system in the crab can be subdivided into three basic subsystems: the detector, the slow-phase system, and the fast-phase system.

(*a*) *The detector*

In the crab statocyst there is a horizontally orientated circular canal which contains fluid and slender thread hairs (Sandeman & Okajima, 1972). During rotation the fluid in the canal is displaced by the imposed angular acceleration, and if the hydronamics of the system are like those of the vertebrate semicircular canals the displacement of the fluid at any instant provides an accurate measure of the instantaneous angular velocity of the canal (Steinhausen, 1933; van Egmond, Groen & Jongkees, 1949; de Vries, 1956; Howland, 1971; Melvill Jones, 1971). The displacement of the fluid deflects the thread hairs, and it is known that the discharge frequency of these receptors is proportional to the extent of their displacement (Sandeman & Okajima, 1972). The output of the statocyst during rotation will therefore be a measure of angular velocity over a range, whose limits are at present being determined.

(*b*) *The slow-phase system*

Observation of the electrical responses of thread-hair neurones and of the resultant electrical activity in the contracting eye muscles shows that the two are often alike in their frequencies and duration. For example, a transient movement of the fluid in

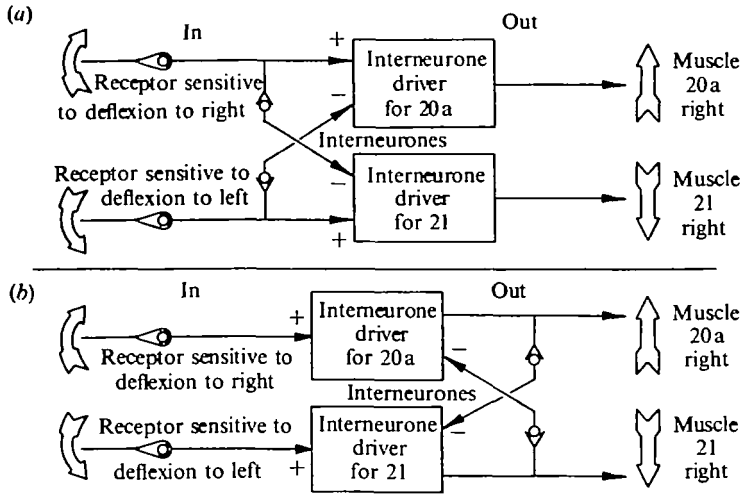

Fig. 10. Two possible arrangements of cross-inhibition between the systems driving the antagonist muscles of one eye. The first shows the inhibition being produced by the directionally sensitive receptors (curved arrows) on the input side of the interneuronal driving system. The second shows the inhibitory cross-over to occur at the output of the driving systems. Only the second model will provide a motor output which will be balanced independent of the sensory input.

the canals produces a discharge of the thread-hair receptor neurones lasting up to 50 sec and in some eye muscles an almost exactly similar response occurs, particularly if it is not interrupted by a fast-phase inhibition. For this reason one may expect to find a fairly direct link between the sensory and motor system similar to that proposed for the vertebrates (Lorente de Nó, 1933; Dohlman, 1938; Spiegel & Price, 1939; Korn & Bennett, 1971).

In addition to the generation of the slow-phase activity in one set of muscles the directional stimulation of the statocyst produces inhibition of the antagonists. The mechanism could involve either a direct inhibition of the slow-phase systems by the directional inputs from the statocyst or a mutual inhibition of the antagonists at their outputs. The two alternatives are shown in Fig. 10, and their essential difference is that the cross-inhibition is on the input side of the interneuronal driving system in the first model and on the output side in the second model. The second model is more attractive when considered together with the fast-phase system (see below).

(*c*) *The fast-phase system*

The simplest view of the fast-phase system is to assume that the driver interneurones producing the slow phase eventually depolarize a fast-phase interneurone sufficiently for it to discharge. This is then fed back to the slow-phase driver interneurone to inhibit it and at the same time excites the antagonist fast-phase driving system for a short time. The model is shown in Fig. 11, indicating the pathways involved during a slow phase of the right eye toward the right side followed by a fast phase to the left. The model includes a cross-inhibitory network on the outputs of the slow-phase driving systems. By itself the cross-inhibitory system will result in

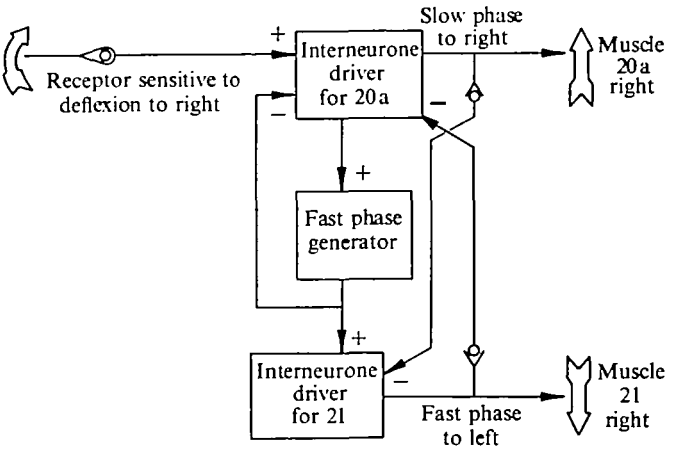

Fig. 11. The slow-phase and fast-phase systems of the right eye. The directional input from the receptor drives the interneuronal driver of muscle 20a and produces a slow phase away from the midline. The output to muscle 21 is inhibited. The interneurone driver of 20a also feeds into the fast-phase generator which fires, transiently inhibits the driver of 20a through its feedback, and vigorously excites the driver of 21 which responds with a burst of impulses, aided by the absence of any inhibition from the 20a driver. The fast-phase generator, having fired its short burst, does not keep on driving the muscle 21 system, but the input from the receptors to 20a continue so that the balance is again tipped gradually in the other direction.

a balance of motor output to the antagonist muscles which is biased in one direction or the other by a directional input. The fast phase has the effect of quickly throwing the balance of the system in the other direction by completely inhibiting the slow-phase driver and vigorously exciting the antagonist. The inhibitory effect of the antagonist upon the slow-phase driving system means that its discharge frequency will be forced back to a low level. However, if the directional input persists the balance of the output will again be forced over. This system implies that the fast phase is not a very short burst of impulses in the one set of muscles but an event which will take some time to occur and produce an overlap of excitation in the antagonist muscles. Myograms show that this is the case; fast-phase discharges, after an initial high-frequency burst, gradually diminish in frequency as the antagonist's slow-phase discharge increases.

That the fast-phase system has access to the same driving system of the eye motoneurones as the slow-phase system is shown by muscle units where activity builds up slowly in frequency during the slow phase but which also give a rapid burst of activity during fast phases in the same direction, and are inhibited in the reverse direction. The point in the system where these operations of excitation and inhibition are carried out has not been discovered. In vertebrates clear inhibition of motor cells during the fast phase has been demonstrated (Baker & Berthoz, 1971; Maeda, Shimazu & Shinoda, 1972) and it has also been found that electrotonic coupling between motoneurones is probably significant for synchronization of motoneurone discharges during the fast phase (Korn & Bennett, 1971). The fast-phase system in crabs, as in vertebrates, is obviously more complex in structure than the slow-phase system because it must include the slow-phase system. Fast phases in crabs were never generated without a preceding slow phase.

SUMMARY

1. The fast and slow eye movements of nystagmus in crabs can be produced by moving a striped pattern around the animal or by rotating the animal in complete darkness. The discharges in the eye muscles are the same regardless of the method used to produce nystagmus.

2. Controlled irrigation of the statocyst in isolated eye–brain preparations of the crab produces activity in the eye muscles which is equivalent to the slow and fast phases of normal nystagmus.

3. When stimulated together, both statocysts combine to produce a greater excitation of the appropriate eye muscles than that produced by the stimulation of a single statocyst.

4. Anticlockwise rotation of the fluid in the *left* statocyst produces greater muscle activity than clockwise rotation of the fluid in that statocyst. Clockwise rotation of the fluid in the *right* statocyst is more effective than anticlockwise rotation in the right statocyst.

5. In a model of the system the mutual inhibitory effect between the systems driving the eyes in opposite directions is placed on the output side. The fast-phase system operates through the slow-phase systems, driving one side vigorously while inhibiting the other.

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