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THE ACTION OF THE EYECUP MUSCLES OF THE CRAB, *CARCINUS*, DURING OPTOKINETIC MOVEMENTS

BY M. BURROWS* AND G. A. HORRIDGE
Gatty Marine Laboratory and Department of Natural History
University of St Andrews

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INTRODUCTION

In decapod crustacea the compound eye lies upon a projecting *eyecup* which is moved by nine eyecup muscles about a flexible joint with the *eyestalk*. Three eyecup reflexes are distinguishable. First, a movement of the whole visual field causes an optokinetic response in which both eyecups follow the stimulus. In the horizontal, but not the vertical, plane there are nystagmus movements in which the eyecups periodically flick back and start the movement over again. Secondly, on tilting the animal, the eyecups tend to hold their absolute position in space. These two responses occur in any direction by a movement at the universal articulation of the eyecup upon the eyestalk. Thirdly, a noxious stimulus on or near an eyecup causes a unilateral withdrawal of that eyecup into its socket. The different movements and stimuli which cause these three reflexes are defined in Fig. 1.

Superimposed on these reflex movements are four other small amplitude movements which occur even when the visual field is stationary.

(1) When the crab is surrounded by a blank visual field the eyecups show *tremor* at a frequency of 2–5 Hz. and amplitude of 0·05–0·2° peak-to-peak (Horridge & Sandeman, 1964). This tremor is sufficient to sharpen perception of contrasting edges (Horridge, 1966*a*). Its control is dealt with in a later paper (Horridge & Burrows, 1968).

(2) Spontaneous *flicks or saccades* occur infrequently with an amplitude similar to tremor but with a fast initial phase and a slow return phase (Horridge, 1966*b*).

(3) When a contrasting object is presented to a crab the eyecups often show *scanning* movements with an amplitude of 0·5–1° peak-to-peak (Horridge & Sandeman, 1964). In *Carcinus* these movements are infrequent but some crabs such as *Pachygraspus*, show a regular oscillatory scan.

(4) In the dark, or when seeing no contrasts, the eyecups *drift* from their original position. At all times there may be a very slow drift, over periods of minutes, back to a 'preferred' position near the centre of the orbit (Horridge & Sandeman, 1964; Horridge, 1966*b*).

Study of the control at the eyecup joint offers many advantages in that several different situations of natural stimulation are available, and it is possible to record the pattern of activity in about 25 motoneurons by intracellular electrodes in the muscle fibres to which they run. Such a system is especially favourable for analysis of how a

* Present address: Department of Biology, University of Oregon, Eugene, Oregon. 97403 U.S.A.

crustacean uses its peripheral neuromuscular system. This paper is concerned with the action and control of the eyecup muscles during a normal optokinetic response.

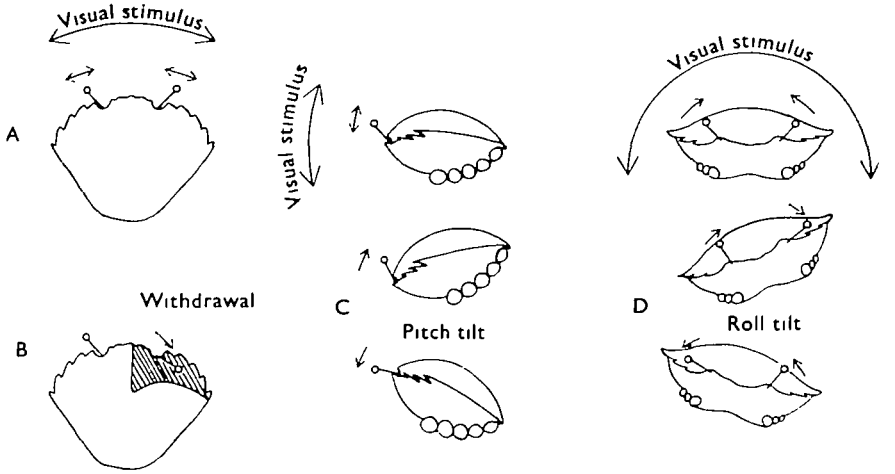

Fig. 1. Eyecup movements. A movement of the whole visual field in any plane causes an optokinetic following movement, which is stronger in the horizontal (A) than in the vertical plane. Nystagmus movements occur only in the horizontal plane. A mechanical stimulus to the carapace (shaded area in B) causes a unilateral withdrawal of the eyecup into its socket. Pitch (C) or roll (D) tilt cause compensatory movements, tending to preserve the absolute position of the eyecup in space. Appropriate movement of the visual field also causes movement in these planes. Only in vertical movements (C) do both eyecups move in the same direction relative to the midline.

METHODS

Anatomy

The eyecup muscles were examined both unfixed and after fixation for 12 hr. in sea-water Bouin. The latter softens the exoskeleton and facilitates dissection of the now coloured and hardened muscles. For histological work the eyecup was perfused with a solution of 2·5% glutaraldehyde in cacodylate-buffered sea water at pH 7·4 and post-fixed in OsO_4 in sea water. Transverse and longitudinal sections at 0·5μm. thick of each muscle were cut from Araldite blocks, and stained with toluidine blue. Attached pieces of exoskeleton enabled the muscles to be orientated, and the same fibres were identifiable in T.S. and L.S.

Motoneurons were demonstrated by staining with methylene blue, while the blood supply to the eyecup was revealed by injecting the main vessels as they leave the heart with indian ink from which shellac is removed (Gunther Wagner 'Pelikan' C11 (1431*a*) (Sandeman, 1967).

Electrophysiology

The intact crab was rigidly held at the lateral edges of its carapace by a clamp which prevented the legs touching the eyecups. The crab was arranged with its transverse axis horizontal and its longitudinal axis 15° above the horizontal at the anterior end, as in the resting posture.

Extracellular muscle action potentials and eyecup movements were recorded simultaneously from the freely moving right eyecup. To reach the muscles, holes were drilled with small entomological pins through the exoskeleton over the appropriate muscle. The end of a small coil of silver wire 50 μm. thick, insulated to the tip, was inserted into

the muscle through the hole. Such an electrode leaves the eyecup free to move but is rarely dislodged, while it records potentials of 100–200 μV. amplitude. After an experiment the electrode wire was cut at its entry into the eyecup, which was then removed and fixed for 12 hr. in sea-water Bouin. Subsequent dissection confirmed the placement of the electrode tip.

To measure eyecup movements, a 2 cm. L-shaped wand of 0·2 mm Nylon line was fixed with Eastman 910 adhesive to the medial side of the eyecup and extended over the carapace of the crab. The wand which carried a stable 40 KHz. 10 V. peak-to-peak signal moved between two metallic antennae which picked up the signal and fed it to a differential a.c.-coupled amplifier. The output of this amplifier was then compared with the original 40 KHz. signal and converted into a d.c. voltage. The system will measure eyecup movements linearly over a range of 30° with a sensitivity of 0·01°, and faithfully up to 10 Hz. (Sandeman, 1968).

A drum with vertical black and white stripes each subtending an angle of 15° at the crab's eye was used as the visual stimulus. Continuous drum movements were available at speeds ranging from 0·03°/sec. to 5°/sec.

Intracellular recordings from the eyecup muscles were made from the right eyecup, firmly cemented in its socket. To avoid interference from objects in the view of this eye, it was blinded by coating the cornea with quick-drying black paint. With this arrangement the right eyecup muscles are driven by the visual stimulation to the left eye. All experiments were performed with the crab in air.

RESULTS

Anatomy

Eye assembly

The complete eye assembly consists of five skeletal elements moved by thirteen pairs of muscles. The terminology is taken from Cochran (1935). Anterior to the brain is the median plate which is moved about the main body skeleton by three pairs of muscles not treated here. Attached to this plate are the elongated eyestalks which project laterally on either side. They are attached proximally to the exoskeleton by membranes along their anterior and posterior edges, and distally by muscle 18 which can move both eyestalks about their longitudinal axes. The eyestalks are completely enclosed by a fold of the carapace and only the eyecups, which attach to their proximal end, normally protrude. In the resting posture the eyecups point forward at an angle of 40–45° to the longitudinal body axis and at 40–45° to the vertical. In this position the rows of ommatidia are horizontal.

Movement of the eyecup upon the eyestalk is possible in all planes, allowing a total excursion of 30° in the horizontal plane (yaw), 70° in the vertical (pitch) and 50° when the crab is rotated about its longitudinal axis (roll). Superimposed photographs of the eyecup during a horizontal movement show that the apparent pivot continually shifts (Fig. 2). As the eyecup moves toward the mid-line the 'pivot point' moves back from near the centre of the eyecup to the distal edge of the eyestalk. This can occur because the joint has no fixed condyles but is surrounded by a flexible arthrodial membrane, and the eyecup is suspended upon its muscles. The arthrodial membrane is stiffened by three small sclerites which attach to the edge of the eyecup and tuck into the membrane (Fig. 3).

Eyecup musculature

The nine eyecup muscles (Fig. 3) have their origins on internal projections of the eyestalk exoskeleton and insert on the eyecup at points which are recognizable externally by a different texture of the surface exoskeleton. The numbering of the muscles described by Cochran (1935) for the American blue crab, *Callinectes sapidus*, has been retained but her nomenclature has been abandoned as it implies certain functions which are not confirmed. According to Cochran's terminology, muscle 19, the oculi abductor and muscle 23, the oculi retractor medialis consist of two branches, a and b, while muscle 20, the oculi retractor dorsalis consists of three parts, a, b and c. The branches of these muscles are found to be separate physiological units but the numbering is retained implying that they have similar origins whatever their function.

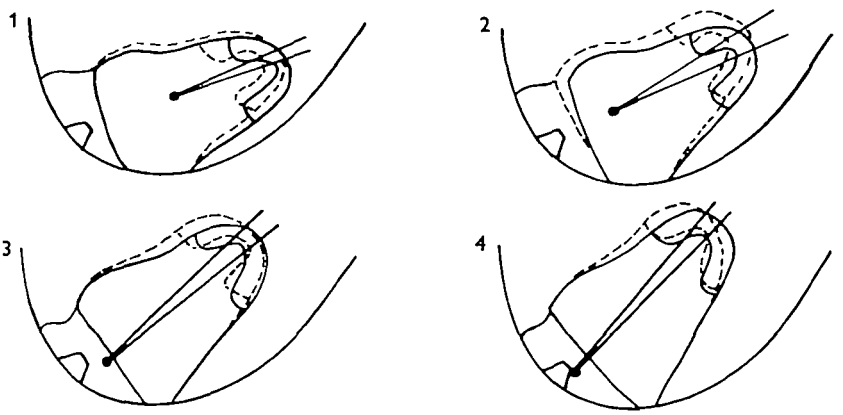

Fig. 2. Tracings from photographs taken vertically above the crab as the right eyecup was moving towards the midline. Several exposures of the eyecup in successive positions were made on the same frame, and the camera was not moved between frames. The first position is shown by the solid line; the second by the dashed line. The 'pivot' point of the eyecup, as found by moving a 'cut-out' figure over the outlines, is not constant, but continually changes during movement.

Muscle 19*a*, the largest in the eyecup, originates at the base of a lateral projection of the eyestalk and inserts on the lateral wall of the eyecup just behind the cornea. All the fibres are of the 'Fibrillenstruktur' type (later shown to be fast or phasic fibres) as described in vertebrates by Kruger (1949), Hess (1961) and in Crustacea by Cohen (1963). The Z-bands, often broken across the width of a fibre, are spaced 3–4 μm. apart.

Muscle 19*b* originates beside 19a on the base of the same projection but runs medially and inserts on the ventral surface of the eyecup. The fibres are not uniform in appearance; some have Z-bands spaced 10–12 μm. apart, as in 'Felderstruktur' fibres elsewhere. The other fibres have an intermediate structure with a sarcomere length of 6–8 μm. Extreme 'Fibrillenstruktur' fibres are not present.

Muscle 20*a* originates on the distal end of the lateral eystalk projection and inserts on the lateral wall of the eyecup behind muscle 19a. The majority of its twenty-five or so muscle fibres have sarcomere lengths of either 3–4 μm., or 10–12 μm., but a few are intermediate. The fibre types are intermingled.

Muscle 20*b* has the same origin as 20a but runs vertically upwards to insert on the dorsal eyecup wall near its proximal edge. This small muscle, enclosed in a tight connective sheath, has approximately ten muscle fibres of which only three have sarcomere lengths of less than 4 μm., the rest being 10–12 μm.

Muscle 20*c* runs vertically downwards from its origin below 20a and 20b to insert

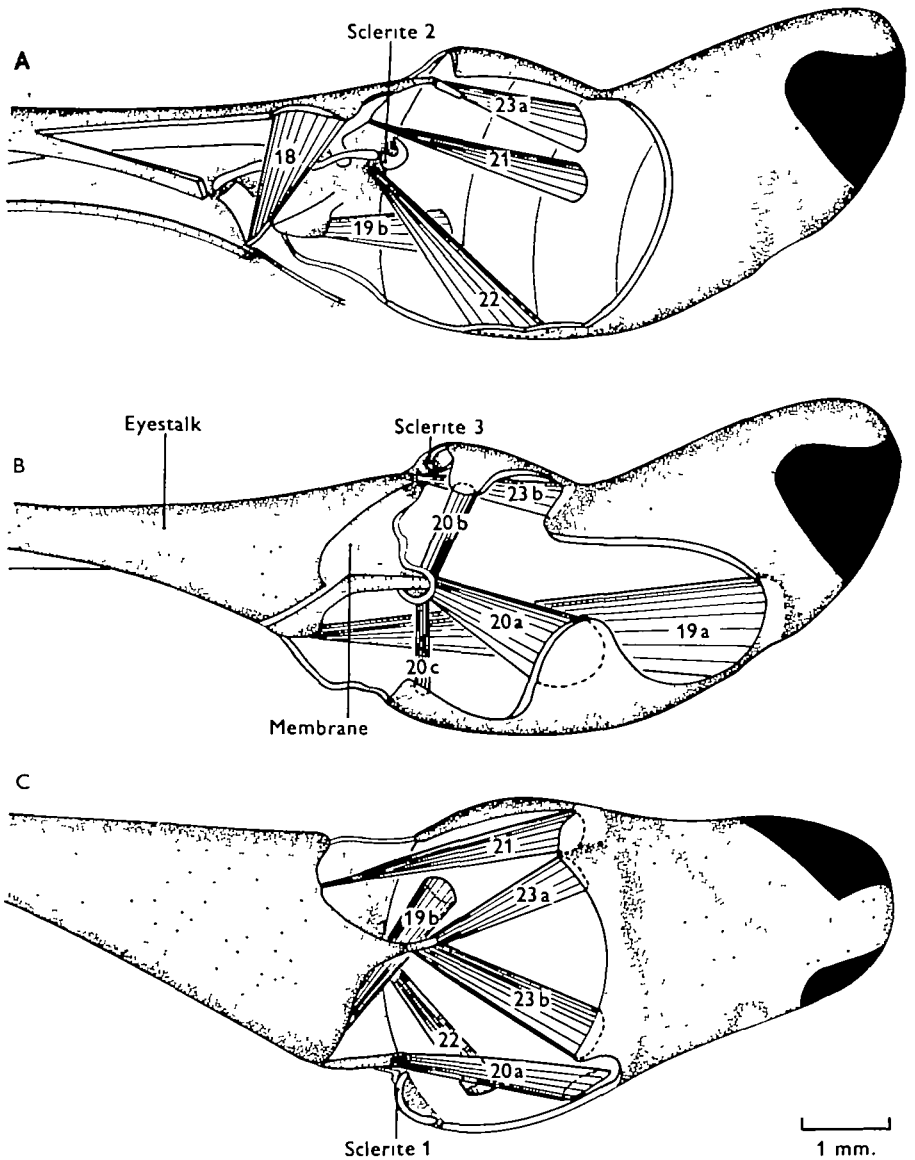

Fig. 3. Musculature of the eyecup and eyestalk in *Carcinus*. (A) Right eyecup dissected from the lateral side to show the medial muscles. (B) Dissection from the same side to show the lateral muscles. (C) Dorsal view with muscles 18, 19a, 20a and 20b omitted. The joint is surrounded by a continuation of the membrane which attaches the eyestalk to the main body skeleton. The membrane is stiffened by three sclerites near the attachment of the muscles to internal projections of the exoskeleton of the eyestalk.

on the ventral wall of the eyecup near its proximal edge. It is smaller than muscle 20b, with about eight fibres, half of which have 'Fibrillenstruktur' and the other half 'Felderstruktur'. Sclerite 1 stiffens the membrane near the attachment of muscles 20a, b and c.

Muscle 21, small and compact, arises from a tendon attached to the medial edge of the eyestalk and inserts in a depression on the medial side of the eyecup. Fibres with 'Fibrillenstruktur' and 'Felderstruktur' are intermingled but few show extreme 'Felderstruktur'.

Muscle 22 runs diagonally across the eyecup from its origin, near sclerite 2 and a skeletal bar, to its insertion on the ventro-lateral wall of the eyecup. The skeletal bar runs in the arthrodial membrane from the sclerite to which muscle 18 attaches. The fibres are predominantly 'Felderstruktur' with sarcomere lengths of 8–10 μm.

Muscle 23*a* has its origin on the medial edge of a prominent jointed projection of the dorsal surface of the eyestalk and inserts above muscle 21 on the dorso-medial surface of the eyecup. Histologically the fibres are a mixed population with the 'Felderstruktur' fibres towards the dorsal surface.

Muscle 23*b* arises alongside muscle 23a and inserts on the lateral side of the dorsal eyecup surface. The joint membrane is stiffened at the origin of these two muscles by the intucking of sclerite 3. The muscle fibres have sarcomere lengths of 6–12 μm.

Muscle 18 is the only muscle present in the eyestalk. It has its origin upon a sclerite which is fixed to the main body skeleton and it spreads to an insertion on the dorsal wall of the eyestalk which it rotates relative to the body. Its fibres are mixed in type.

Innervation of the muscles

After leaving the brain the oculomotor nerve branches before entering the eyestalk and a small purely sensory lower branch ramifies in connective tissue and supplies the carapace around the eyestalk. The upper branch, containing about thirty large axons, runs in the hollow of the eyestalk until, at the level of muscle 18, it branches profusely to the eyecup muscles. The optic tract branches at the same level and also supplies some of the eyecup muscles. The branches of both these nerve trunks are so interwoven that a complete picture, with anatomical origins and numbers of axons, for each muscle cannot be given. Methylene blue staining has been most successful for muscle 20a, which receives four axons from the oculomotor nerve, and a large axon from the optic tract which also supplies muscles 19a and 19b.

Proprioceptive structures, although sought in methylene blue studies and in serial transverse and longitudinal sections of the eyecup, have not been found. However bipolar cells of unknown function but typical of many arthrodial membranes have been described in the membrane of the eyecup/eyestalk joint (Sandeman, 1964).

Blood supply to the eyecup

The eyecup is supplied by branches of two blood vessels. The optic artery which runs along the anterior edge of the eyestalk supplies the optic lobes (Sandeman, 1967) but also branches to supply muscles 20a, b and c, 23a and b and muscle 21. The oculomotor artery runs along the posterior edge of the eystalk and supplies the rest of the musculature but also muscle 21 as well. Visual reflexes fail soon after the blood vessels are damaged.

The optokinetic response

Continuous horizontal rotation of the vertically striped drum around the crab induces an optokinetic nystagmus. This consists of a slow forward phase, in which both eyecups follow the direction of the drum rotation but with an ever-increasing lag, and a fast return phase (flick-back) which returns the eyecups approximately to their original position, from which they repeat the cycle. The two eyecups move together, but in opposite directions relative to the midline of the crab. Drum speeds of 2·2°/sec have been used in most of the records figured here, but tonic responses are similar at drum speeds from 0·001°/sec to 5°/sec.

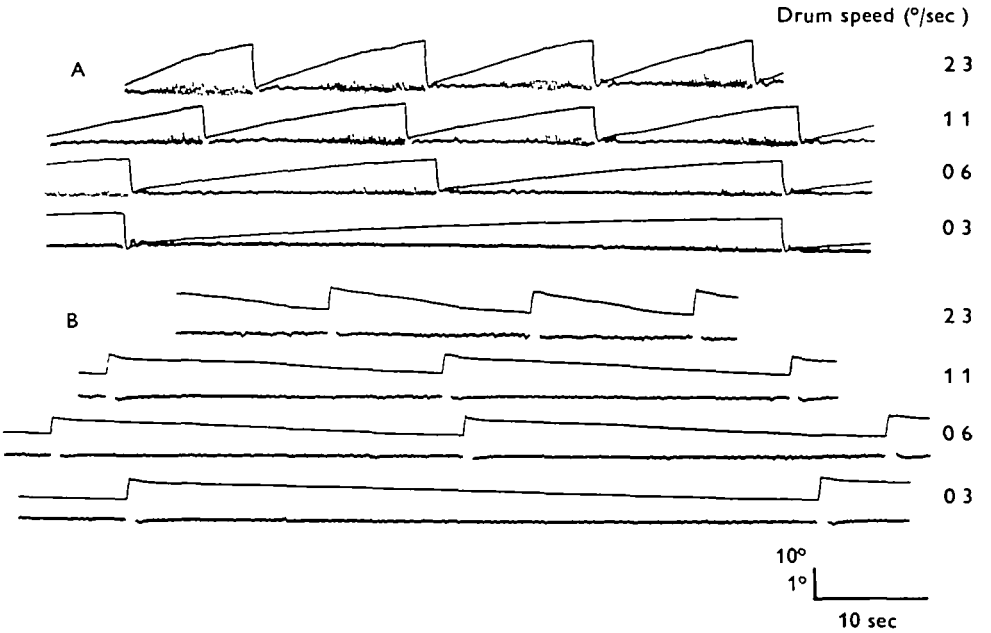

Fig. 4. Nystagmus movements of the right eyecup of one crab recorded as it followed the continuous rotation of a striped drum moving at various speeds. In (A) the drum moved clockwise so that the slow-phase eyecup movement was away from the midline; in (B) the drum movement is reversed and the baseline is adjusted. The upper trace represents the d.c. component of the eyecup movement while the lower is a.c.-coupled at ten times the amplification to reveal tremor. During the course of a slow phase the tremor increases both in frequency and amplitude, but is less at lower drum speeds and when the eyecup moves toward the midline.

The slow phase

The eyecup response during the slow phase is not a simple representation of the drum movement. When the eyecup starts from rest after a previous flick-back it moves faster than the drum but soon slows to a uniform speed which is less than the drum speed (Fig. 4). Towards the end of the slow phase the eyecup slows down and frequently may stop some time before the next flick-back occurs. Neither the actual stimulus to the eye (the difference between drum speed and eyecup speed, which is termed the slip speed) nor the ratio of response velocity to actual stimulus velocity (termed the velocity gain of the system) is constant during a single slow phase. Furthermore, tremor of the eyecup is initially of a low frequency and amplitude, but about

halfway through the slow phase it increases in both frequency and amplitude. Tremor is smaller in amplitude when the eyecup moves toward rather than away from the midline, and is smaller at lower drum speeds (Fig. 4). Tremor is correlated with the activity of fast motoneurons to two muscles subsequently to be described. The total extent of the slow phase can vary from 2 to 20° with a mean of 10°, and in a series of nystagmus movements by one eye its exact form sometimes shows great variation, even at a constant drum speed. Other animals, however, are remarkably consistent in performance over periods of hours. With opposite directions of drum rotation the slow phase occurs over different ranges of the orbit, with the fast phase in either direction restoring the eyecups to the same approximately central position.

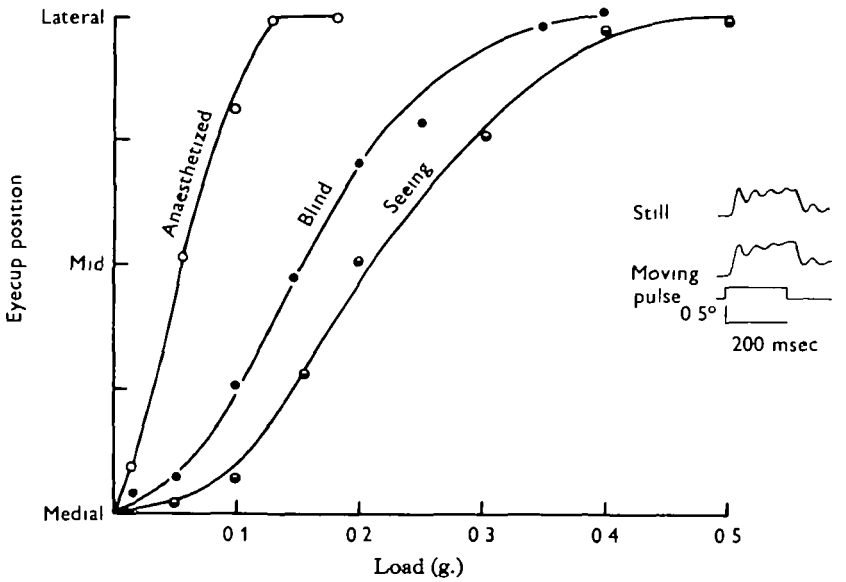

Fig. 5. Graphs of load imposed on the eyecup and its resulting deflexion in anaesthetized, blind and normal crabs. The curve for anaesthetized crabs represents the force necessary to overcome the passive elements of the joint, while the difference between the curves for seeing and blind crabs represents the effectiveness of visual feedback. The inset shows the effect of applying a weak pulse by an electromagnet acting on a small piece of iron attached to the eyecup while stationary and while moving through the same point. The equality of the mechanical responses shows that the forces which oppose movement are similar in the resting and in the moving eyecup.

The fast phase

The eyecup movement during the fast phase is relatively uniform but is slightly decelerated towards the end. The movement is constant over the range of drum speeds used. This differs from the situation in the rabbit where there is a correlation between the speeds in the fast and slow phases (Koike, 1959).

Mechanics of horizontal movement

The mechanical characteristics of the eyestalk-eyecup joint during horizontal movement are required before it can be shown that the motor impulse frequency determines the eyecup position. Measurements were made on anaesthetized, blind and normal crabs. One group of crabs was blinded by coating both eyes with black paint, and other,

untreated animals were surrounded by a black and white, vertically striped drum. Small weights were hung on the eyecup by means of a pulley system and the resulting angular deflexion of the eyecup was measured as described in the methods section. Over a range of 15° around the centre of the orbit the deflexion is proportional to the load, but towards the extremities the resistance to movement increases (Fig. 5). In the anaesthetized crabs a torque of 6 dyne-cm/deg. is required to move the eyecup in the central region of the orbit, corresponding to the passive resistance of the joint and muscles. In the blind crab, with background activity in the muscles, the torque needed rises to 20 dyne-cm/deg. and in the seeing eye it is greatest, at 40 dyne-cm/deg. The difference between the curves for blind and seeing crabs is caused by the visual feedback.

To test whether the relation between movement of the eyecup and tension in the muscles applies to the moving as well as to the stationary eyecup, a further check is necessary because the stationary eyecup is not characterized by inactive muscles. A light iron wand was attached to the eyecup and its movements were monitored as previously described. The output of the movement detector system triggered an electromagnet when the eyecup reached a given point, and a sudden impetus of 200 msec. duration at a just effective strength was then applied to the eyecup in the same direction as the eyecup movement. The rise time and amplitude of the resulting small additional deflexion proved to be independent of the position of the eyecup in the orbit or whether it was stationary or moving (Fig. 5). From this it is reasonable to conclude that the resistance of the eyecup joint to deflexion by its own muscles is not greatly increased or decreased by its own movement. Therefore measurements of the effective torques for the stationary eyecup apply to the moving eyecup. Therefore greater muscle tension, so long as it is not antagonized by other muscles, is the cause of greater deflexion of both stationary and moving eyecups.

Electrical activity of the muscles

Two types of responses are recorded from each muscle. The first is a steady tonic activity when the eyecup is stationary or moving, and could be caused by the discharge of a classical 'slow' axon. The second is a 'bursty' or phasic activity usually present only when the eyecup is moving, and which could be caused by the discharge of a classical 'fast' axon. Extracellular records showed that these two types of activity could sometimes be recorded from different parts of a muscle. For example, in muscle 23b, tonic activity is recorded on the dorsal surface and is correlated with the distribution of 'Felderstruktur' fibres. These factors suggest that the fast and slow motor axons to each muscle tend to supply two separate groups of fibres.

Other differences between muscle fibres were noted when recording with intracellular electrodes. On the basis of their membrane properties and innervation patterns the muscle fibres can be somewhat arbitrarily grouped into three main classes, as in leg muscles (Atwood, 1963, 1965); phasic fibres which are supplied only by a fast axon; tonic fibres which are supplied only by a slow axon and intermediate fibres which are supplied by both types of axon.

Phasic muscle fibres have a resting potential between 65 and 80 mV., large junction potentials up to 20–30 mV., with a short rise time, and a time constant of decay of 20–50 msec. (Fig. 6A). The phasic junction potentials show marked facilitation and

at high frequencies spikes may occur, although this shows some seasonal dependence correlated with the moult cycle, as has been found previously (Atwood, Hoyle & Smyth, 1965; Hoyle & Wiersma, 1958*b*).

Tonic muscle fibres usually have a smaller resting potential of 50–65 mV., smaller junction potentials of 5–15 mV., with a slower rise time, and a longer time constant of decay of 50–200 msec. (Fig. 6B). They show little facilitation and at high frequencies

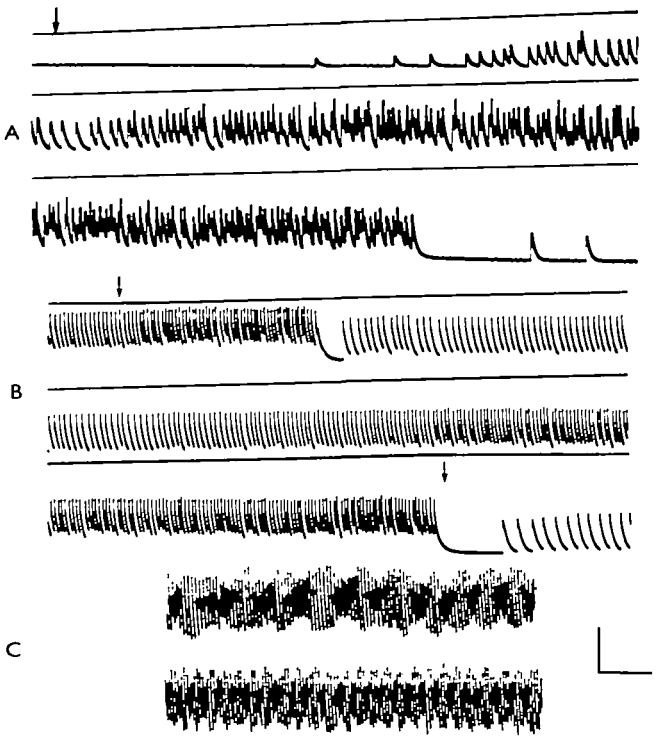

Fig. 6. Intracellular activity recorded from phasic (A) and tonic (B) fibres of muscle 20a of a right eyecup innervated respectively by fast and by slow motoneurones. The records show an optokinetic nystagmus elicited by the rotation of a striped drum, which begins as indicated by the arrows. Phasic activity is absent when the drum is stationary and begins only when the drum has moved a certain distance. The junction potentials then show a gradual increase in frequency with much facilitation. At high frequencies the firing becomes more irregular and active membrane events occur. Tonic activity is present when the drum is stationary and as the slow phase progresses there is an increase in frequency with little facilitation. At high frequencies the activity becomes more regular. All activity is inhibited centrally at the onset of a fast phase movement. (C) A fibre innervated by two slow axons often shows 'beats' caused by the slightly different frequencies of the two axons. As their firing frequency increases so does the 'beat' frequency. Scale: A: 40 mV., 200 msec.; B: 40 mV., 400 msec. C: 10 mV., 500 msec.

the amplitude of the individual junction potentials may decrease as a depolarization plateau is reached. At high firing frequencies fibres innervated by two slow axons often show a 'beat' frequency (Fig. 6C), which is the consequence of two slow axons firing at slightly different frequencies (Katz, 1936).

In intermediate fibres the junction potentials of the slow and fast axons can vary considerably from fibre to fibre. In some, the junction potential of the slow axon is

larger than that of the fast axon; in others the situation is reversed as is found in leg muscles (Hoyle & Wiersma, 1958*a*; Atwood, 1963).

Individual muscle responses

Detailed data is presented in the illustrations which are chosen from many recordings to be representative of the action of the individual muscles.

Muscle 18. This muscle does not directly control movement of the eyecup but governs the rotation of the eyestalk about the main body skeleton. However, a rotation of the eyestalk also results in a slight rotation of the extended eyecup.

During horizontal optokinetic movements of the eyecup tonic activity, due to the firing of a single slow axon, continues at a frequency of about 25 Hz. unaffected by the direction of movement or by the slow or fast phases of nystagmus.

The fast axon to this muscle runs in the optic tract and is active only during a withdrawal movement of the eyecup.

Muscle 19*a*. Many penetrations of fibres of muscle 19a, both with extracellular and intracellular electrodes, have failed to reveal any electrical activity during optokinetic movements. This muscle is, however, involved in withdrawal of the eyecup into its socket, and is dealt with under eyecup withdrawal in a later paper (Burrows & Horridge, 1968).

Muscle 19*b*. Tonic activity in muscle 19b caused by the discharge of a single slow axon occurs throughout optokinetic movements in the horizontal plane. During the slow phase of a response away from the midline the frequency declines very gradually from 20 Hz. (Fig. 7). At the onset of the fast return phase the frequency rises to 30 Hz. and stays at that frequency for the duration of the fast phase, declining again during the course of the next slow phase.

During a slow phase towards the midline the tonic frequency increases slightly from 15 to 20 Hz. (Fig. 8). Just before and for the first 100 msec. of the fast return phase the activity is inhibited but then resumes at its previous frequency. Repeated probing with intracellular electrodes in this and the other eyecup muscles has failed to reveal any evidence of peripheral inhibitory axons. Moreover, records of oculomotor nerve discharges show that the firing of certain axons active in the slow phase of nystagmus is shut off during the fast phase. From this it is concluded that inhibition of the motor output to the eyecup muscles always occurs centrally.

Unlike the phasic potentials of other muscles those in muscle 19b caused by a single fast axon show little change in amplitude by facilitation, and with extracellular leads are always recorded together with the tonic potentials. This is correlated with the lack of extreme 'Fibrillenstruktur' muscle fibres and by a greater similarity in the discharge of the slow and fast axons.

About 100 msec. before the onset of a fast phase toward the midline there is a burst of phasic muscle potentials (Fig. 7). These reach a peak frequency of 60 Hz. before the fast phase movement begins, and then continue at an ever-declining frequency during the fast phase and the next slow phase.

During a slow phase movement toward the midline the phasic activity gradually increases to reach a peak frequency of 20 Hz. midway through the traverse of the eyecup (Fig. 8). This frequency is maintained until activity is centrally inhibited *before* the start of the fast return phase.

Muscle 20a. Two slow axons supply muscle 20a. The frequency of discharge of both depends on the position of the stationary eyecup in the horizontal plane. During a slow forward phase away from the midline the tonic muscle potentials increase evenly in frequency to a maximum of 50 Hz. about mid-way through the traverse of the eyecup (Fig. 9). This frequency is then maintained until 50 msec. before the next fast phase, for the duration of which the activity is inhibited centrally. After the fast phase the muscle potentials resume at three-quarters of their maximum amplitude and gradually increase to full amplitude as the frequency again builds up during the next slow phase.

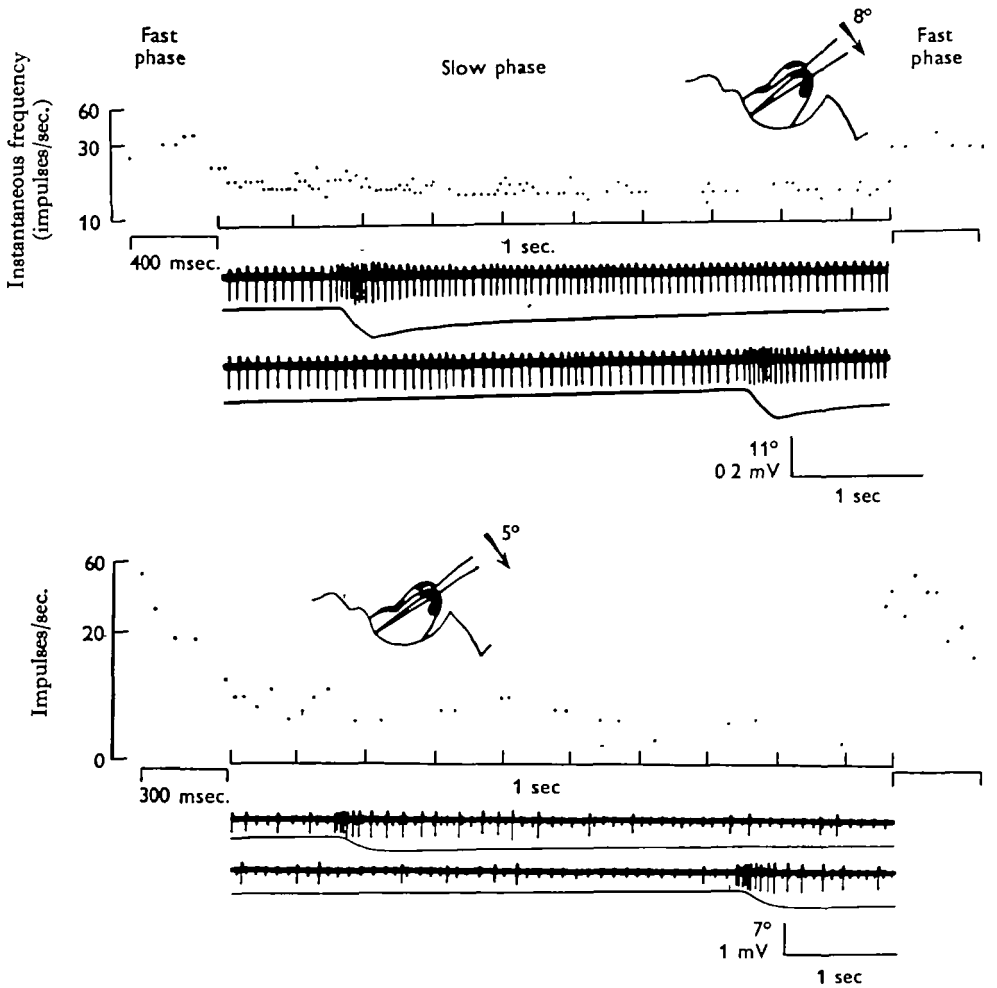

Fig. 7. Tonic (upper) and phasic (lower) activity in muscle 19b during a slow-phase movement of the eyecup away from the midline and a fast return phase toward the midline. On this and subsequent figures each dot shows the instantaneous muscle potential frequency plotted on a logarithmic scale at the instant halfway between two potentials. The time scale for the fast phase is expanded and the inset shows the extent and direction of the slow phase. The lower traces on a different time scale, are the extracellular muscle potential records, from which the graphs were plotted, together with the concomitant eyecup movement. The tonic frequency of muscle 19b declines gradually during the slow phase but is raised during the fast. A burst of phasic activity precedes the fast phase but then gradually declines during the next slow phase.

Two fast axons also supply muscle 20a so that in all this muscle receives at least five axons: four involved in optokinetic movements and one involved only in withdrawal of the eyecup. The two fast axon discharges are usually not recorded when the eyecup is stationary. During a slow phase away from the midline the phasic potentials begin only when tonic activity has reached a high level (Fig. 9). At this time the phasic muscle potentials are barely visible above noise, but as they increase in frequency, they

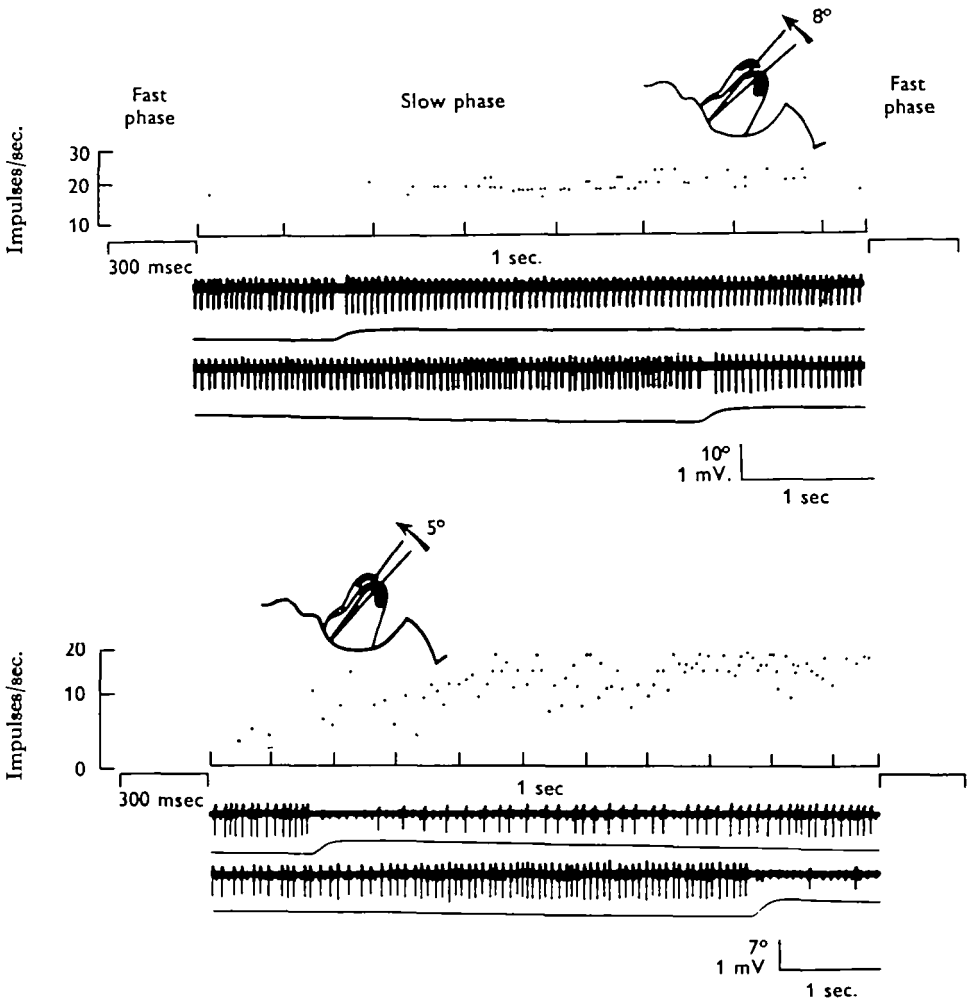

Fig. 8. Tonic (upper) and phasic (lower) activity in muscle 19b during a slow-phase movement toward the midline and a fast return phase away from the midline. Tonic activity increases toward the end of the slow phase and is inhibited centrally during the fast. Phasic activity increases to a peak of 20 Hz. midway through the slow phase and again is inhibited centrally during the fast phase. The phasic potentials show little growth in amplitude by facilitation.

also increase in amplitude. This is not due to the wire electrode being pulled closer to the active muscle fibre, but is due to neuromuscular facilitation, for there is a correlation between the interval between two potentials and the increment of the second potential. This relation is confirmed with intracellular recording (Fig. 6A). The

maximum frequency of 100 Hz. is not reached until near the end of the slow phase. The phasic activity, like the tonic, is inhibited centrally just before and throughout the fast return phase.

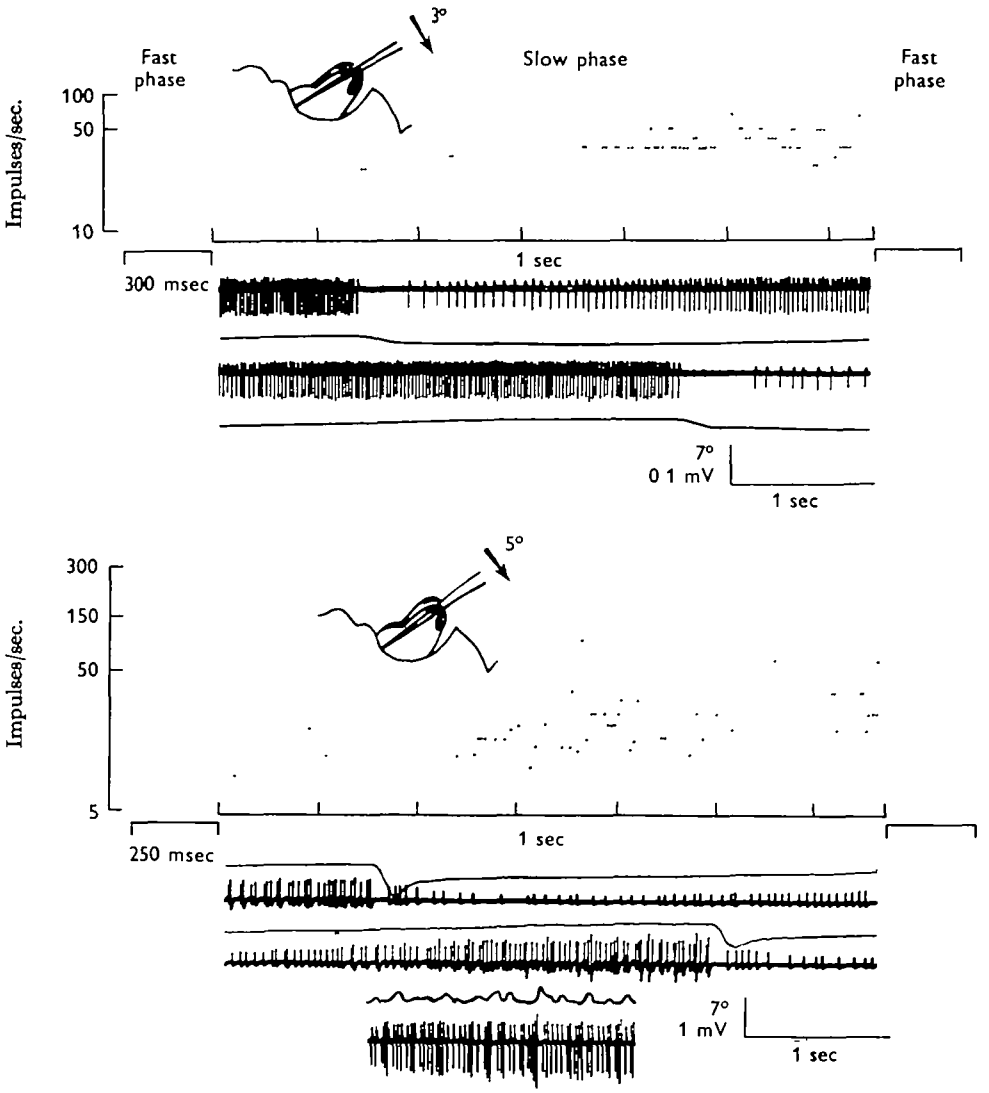

Fig. 9. Tonic (upper) and phasic (lower) activity in muscle 20a during a slow-phase nystagmus movement away from the midline and a fast return phase toward the midline. The tonic muscle potentials gradually increase in frequency with little growth in amplitude by facilitation, and at high frequencies the firing becomes more even. By contrast the phasic potentials facilitate greatly and at high frequencies the firing becomes more irregular. The doublets and groups of potentials are associated with tremor movement of the eyecup. Activity is inhibited centrally just before the fast phase. The group of phasic potentials which occur after the fast phase are associated with the initial spurt of the next slow-phase movement.

After the fast phase a group of potentials may occur which are associated with the initial rapid movement of the eyecup as it sets off on the next slow phase. This unusually high frequency at the beginning of a slow phase can be related to the burst

of speed at the beginning of an optokinetic response when a rotation of the drum is first started. Records from muscle 20a, taken with both eyecups clamped to eliminate visual feedback, reveal a temporary small increase in frequency at the beginning of the slow phase. Whatever its nature, which may be post-inhibitory rebound of some kind, this burst is therefore a part of the central programme. In freely moving eyes the

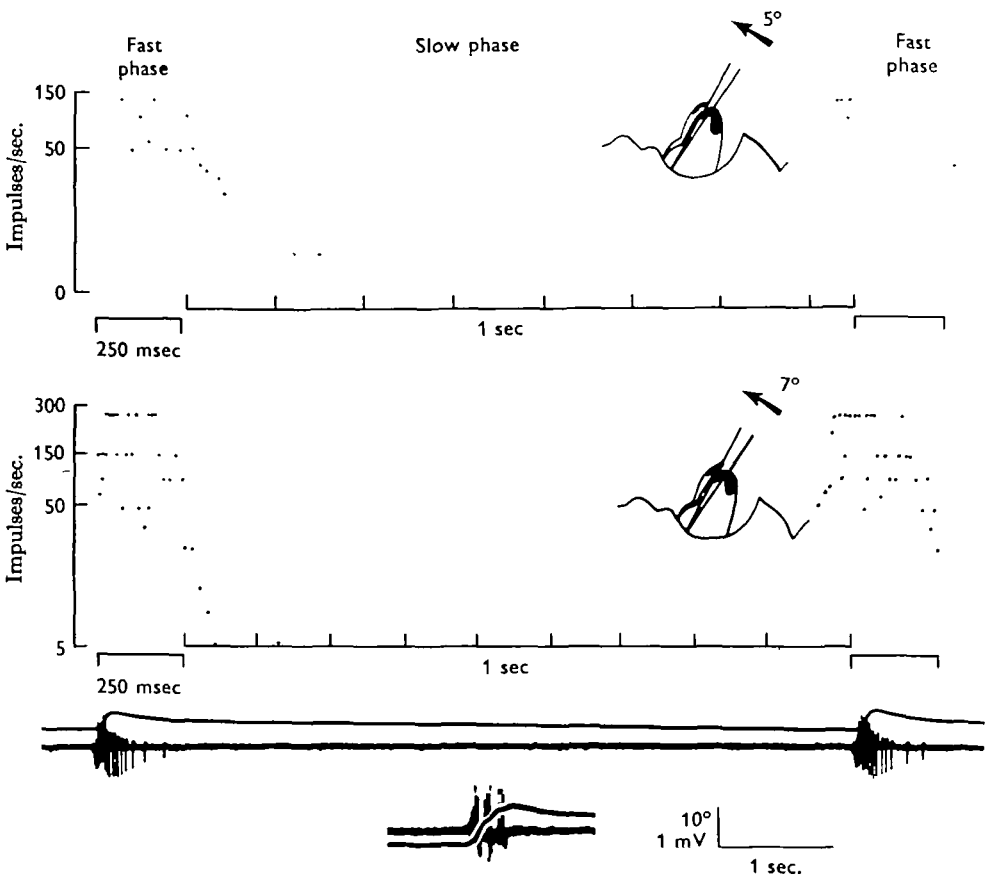

Fig. 10. Activity in tonic fibres (upper) and phasic fibres (lower) in muscle 20a during a slow-phase nystagmus movement towards the midline and a fast return phase away from the midline. Activity in both fibres is confined to bursts which begin just before the fast phase. The tonic activity reaches a peak frequency of 50–100 Hz. and declines slowly, whereas the phasic activity reaches 200 Hz. but declines abruptly. That the latter is a mechanical cause of the fast-phase movement is seen at times when the movement is jerky (inset).

effect is easier to demonstrate and can, in addition, be attributed to the latency in the visual feedback loop, before the eyecup movement gets under way. Small overshoots in eyecup-movement records therefore arise from at least two sources.

When they occur at high frequencies, the phasic potentials caused by a single fast axon show a marked temporal patterning, with an unusually high number of closely spaced groups and pairs of impulses. This tendency is shown in an increased relative variance at the higher frequencies and is in direct contrast to the tonic activity which becomes more uniform at higher frequencies (Fig. 9). The pattern of impulses is not

without effect, for the marked grouping in the later part of a slow phase is accompanied by tremor of the eyecup which is as large as that known to influence the perception of contrasting objects (Fig. 9). When both eyecups are clamped the intracellular activity in muscle 20a corresponds exactly to that recorded in a freely moving eyecup, so that whether the eyecup actually moves or not has no effect on the central mechanism which governs either the average frequency of motor impulses and hence eyecup position, or their grouping which governs tremor. When the seeing eyecup is clamped, the slip speed is constant throughout so that the onset of the phasic activity and its progressive growth and patterning cannot depend on the visual stimulus at that time. Muscle stretch is of no importance because the eye can be clamped in any abnormal position without effect on the motor impulse pattern. There seems to be no alternative to the conclusion that all aspects of the phasic activity, including its onset, are governed by a completely central mechanism which is dependent solely on the velocity and extent of the visual input since the last fast phase. Such a mechanism also governs the frequency reached by the slow motor impulses to this muscle.

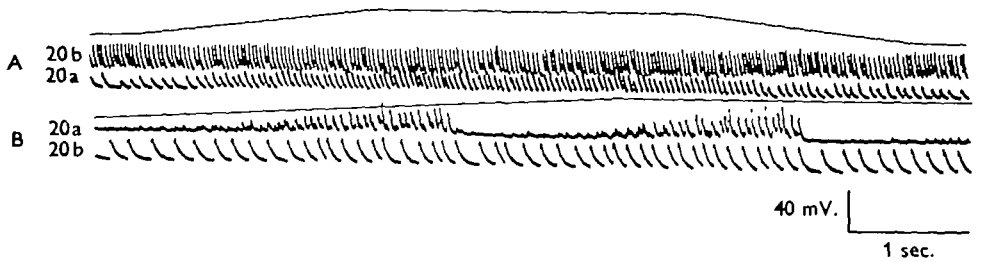

Fig. 11. (A) Intracellular activity in muscle 20b (middle trace) recorded simultaneously with that in muscle 20a (lower trace) during optokinetic responses of the right eyecup. Ramp movements of the drum (upper trace downwards is towards midline) cause no change in the tonic activity of 20b but that of 20a is changed. (B) Phasic responses of muscle 20a (upper trace) recorded with the phasic activity in 20b (lower trace) which changes relatively little during nystagmus.

When the slow phase is toward the midline (Fig. 10) the tonic activity begins just before the start of the fast-phase movement and reaches a peak frequency of 50–100 Hz. during this phase, declining slowly during the first quarter of the next slow phase. Similarly, the phasic activity begins about 50 msec. before the start of the fast phase and reaches a peak frequency of 200 Hz. during this phase, but then declines abruptly (Fig. 10). The phasic activity can be directly linked to the fast-phase movement away from the midline, especially when this movement is jerky, and must be considered to be the prime cause of the movement.

Muscles 20b and 20c. These muscles consist of only eight to ten fibres and are each supplied by a fast and a slow axon, but since they lie close to other eyecup muscles there was always the possibility that activity recorded with extracellular electrodes had spread from the larger neighbouring muscles. Intracellular recordings can be made, but only from a clamped eyecup. Activity is then related to inferred eyecup movement by recording simultaneously from another muscle whose activity has been linked previously to eyecup movement.

Tonic activity in muscles 20b and 20c occurs rather irregularly at a frequency of

about 10 Hz. throughout optokinetic movements in the horizontal plane (Fig. 11A). Phasic activity is also irregular but that in muscle 20b may show a slight increase in frequency during a slow-phase movement away from the midline and a corresponding decrease during movement towards the midline (Fig. 11B).

Muscle 21. Tonic activity in muscle 21 is present in the stationary eyecup at a frequency which depends on the horizontal position of the eyecup in space. During a slow-phase movement towards the midline the activity increases evenly to about 40 Hz. (Fig. 12) and is inhibited centrally just before and for the duration of the fast return phase. Afterwards the muscle potentials resume at their previous amplitude.

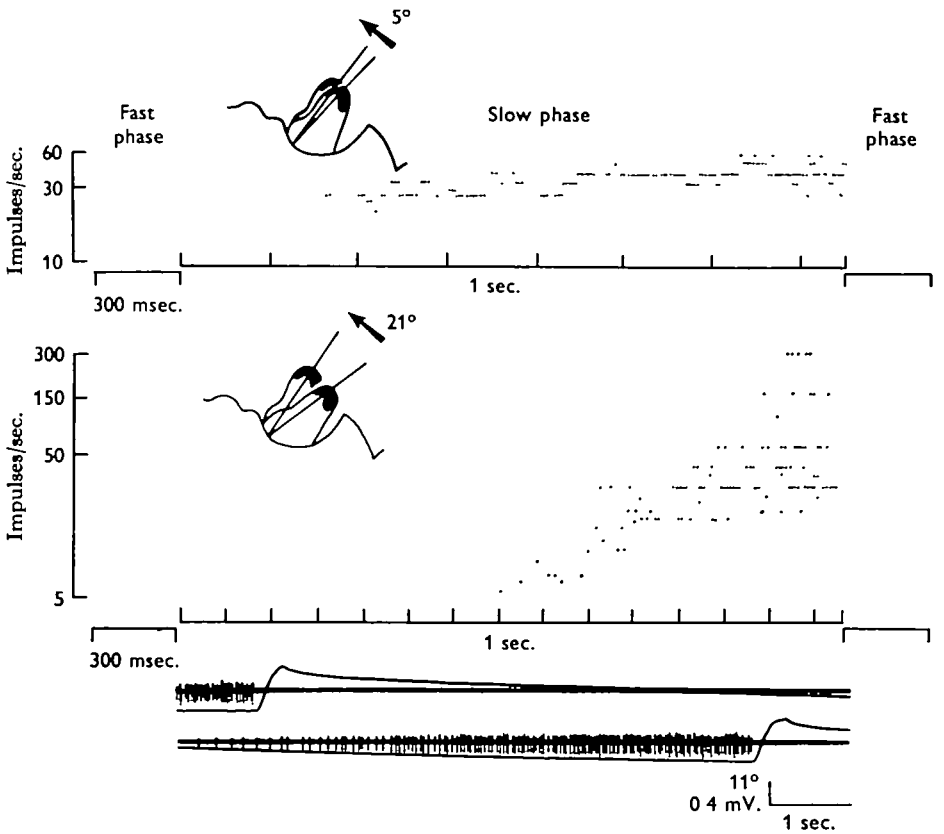

Fig. 12. Tonic (upper) and phasic (lower) activity recorded from muscle 21 during a slow forward-phase movement toward the midline. During the slow phase the tonic potentials show an even increase in frequency but are inhibited centrally during the fast phase. Phasic activity begins only when the eyecup movement is half completed and shows an erratic increase in frequency up to 200 Hz. Again it is inhibited centrally before the start of the fast phase. Scatter in the instantaneous frequency curve for phasic activity increases at the high frequencies, in contrast to that for the tonic activity which becomes more regular.

Phasic activity begins only when the tonic activity has reached a high frequency and when more than half the slow-phase movement has occurred (Fig. 12). The facilitating potentials increase to a peak frequency of 200 Hz. but are inhibited centrally just before the start of the next fast phase. As for the phasic activity of muscle 20a during movement in the opposite direction, the muscle action potentials, caused by the dis-

charge of a single fast axon, tend to occur in groups and doublets which are associated with tremor of the eyecup. At high frequencies the interval scatter increases. This is in direct contrast to intervals between tonic potentials, which become more uniform (Fig. 12).

During a slow-phase movement away from the midline muscle 21 is inactive until just before the onset of a fast return phase towards the midline, when there is a burst of activity in the slow axon (Fig. 13). This reaches a frequency of 60 Hz. and declines gradually during the remainder of the fast phase and the first quarter of the next slow phase. Tonic activity is then completely absent until the start of the next fast phase.

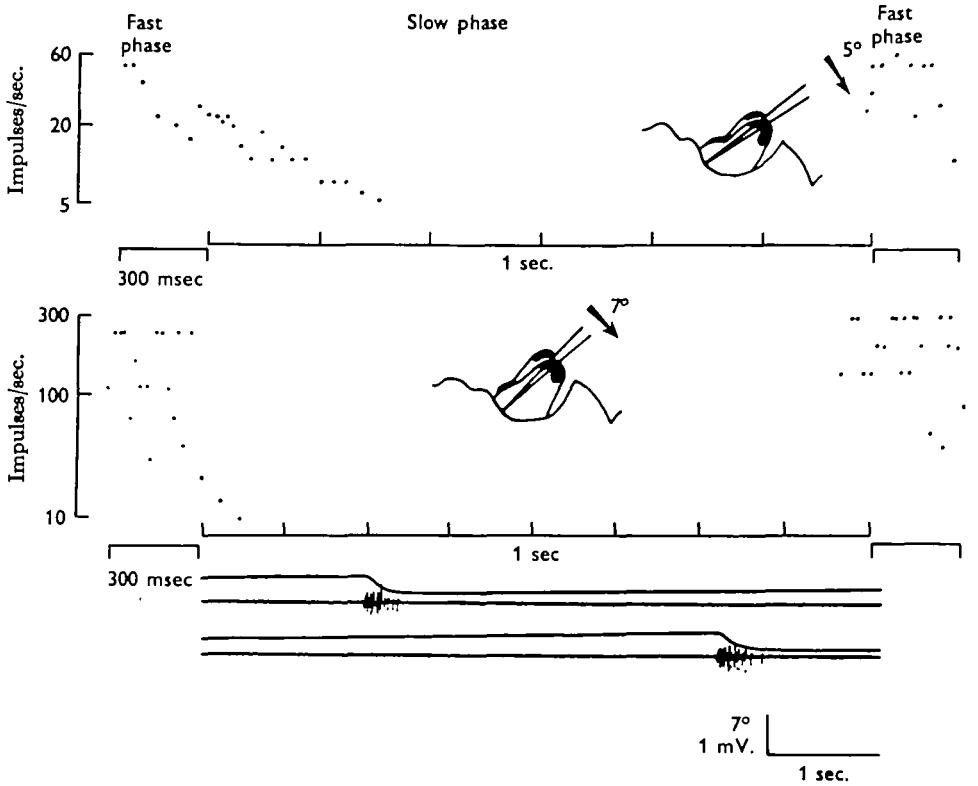

Fig. 13. Tonic (upper) and phasic (lower) activity in muscle 21 during a slow-phase movement away from the midline and a fast return phase toward the midline. Both types of activity occur as bursts before the onset of the fast phase. Tonic activity reaches a peak frequency of 60 Hz. and slowly declines while phasic activity, the prime cause of the movement, reaches a peak of 200 Hz. and declines abruptly.

Similarly, no phasic activity is recorded during the slow forward movement away from the midline until a burst occurs 50–100 msec. before the start of the fast return phase (Fig. 13). The frequency initially reaches 200 Hz. and is maintained briefly at 100 Hz. before declining rapidly. This activity is the main cause of the fast-phase movement.

Muscle 22. During a slow-phase movement of the eyecup away from the midline the frequency of the slow axon discharge to muscle 22 increases only slightly from 10–20 to 20–25 Hz. (Fig. 14). Just before the fast return phase the activity is inhibited

centrally but is suppressed for only the first 100 msec. of the 300 msec. long fast phase. During the last two-thirds of the fast phase a group of muscle potentials occur at a frequency of 25–30 Hz., which is higher than the maximum achieved during the slow phase.

During a slow-phase movement towards the midline there is no change in tonic background activity of 10–20 Hz., but during a fast return phase the frequency is raised to 50 Hz. (Fig. 15).

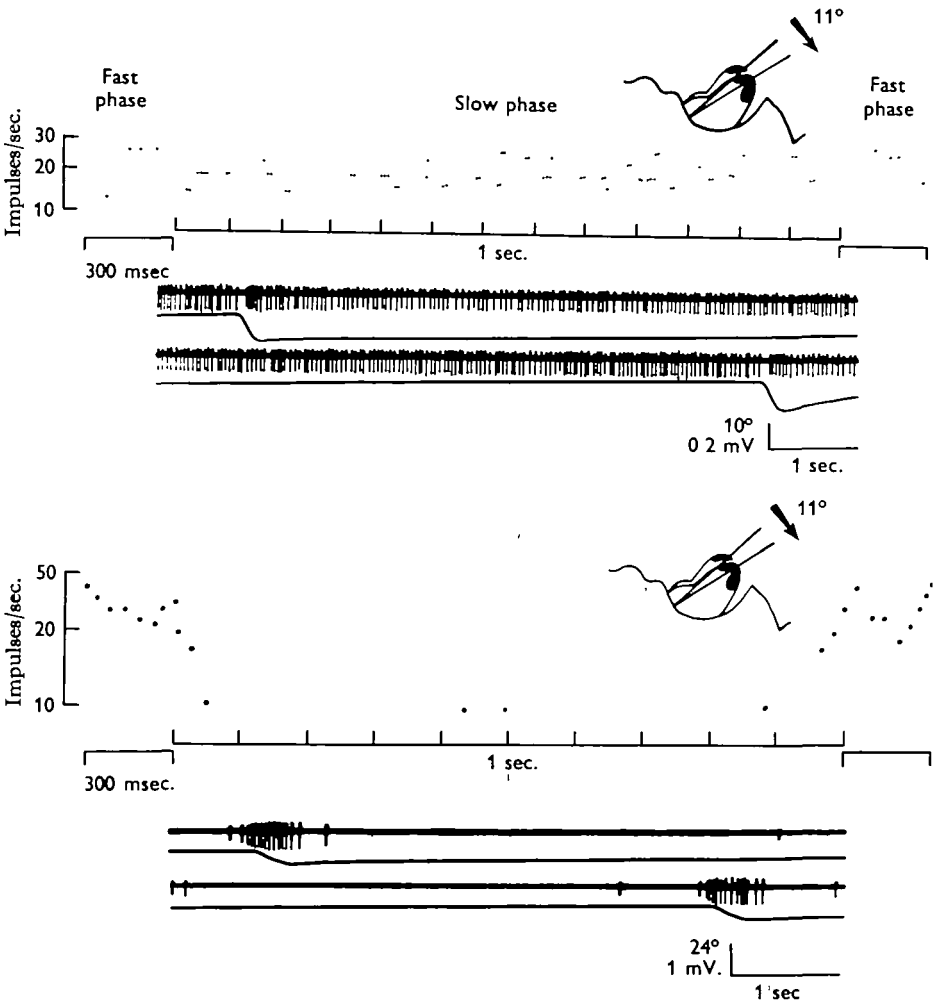

Fig. 14. Tonic (upper) and phasic (lower) activity in muscle 22 during a slow-phase movement away from the midline and a fast return phase toward the midline. The tonic potentials gradually increase in frequency during the slow phase and are inhibited centrally during the fast. A burst of phasic activity begins 100 msec. before the start of the fast phase and reaches a peak of 50 Hz.

Phasic activity in muscle 22, due to the discharge of a single fast axon, is limited to a few potentials at a low frequency, during the greater part of slow-phase movements in either direction. However, about 100 msec. before a fast phase towards the midline a burst of potentials occurs which approaches a peak frequency of 50 Hz., lasts for

the duration of the fast phase and declines during the first 200 msec. of the next slow phase (Fig. 14). There is also a burst of a few facilitating muscle potentials at a frequency of about 20 Hz. starting *after* a fast-phase movement away from the midline has been initiated, primarily by muscle 20a (Fig. 15).

Muscle 23a. The discharge of the slow axon to muscle 23a is more regular than that of the slow axon to muscle 22. Throughout a slow-phase movement away from the

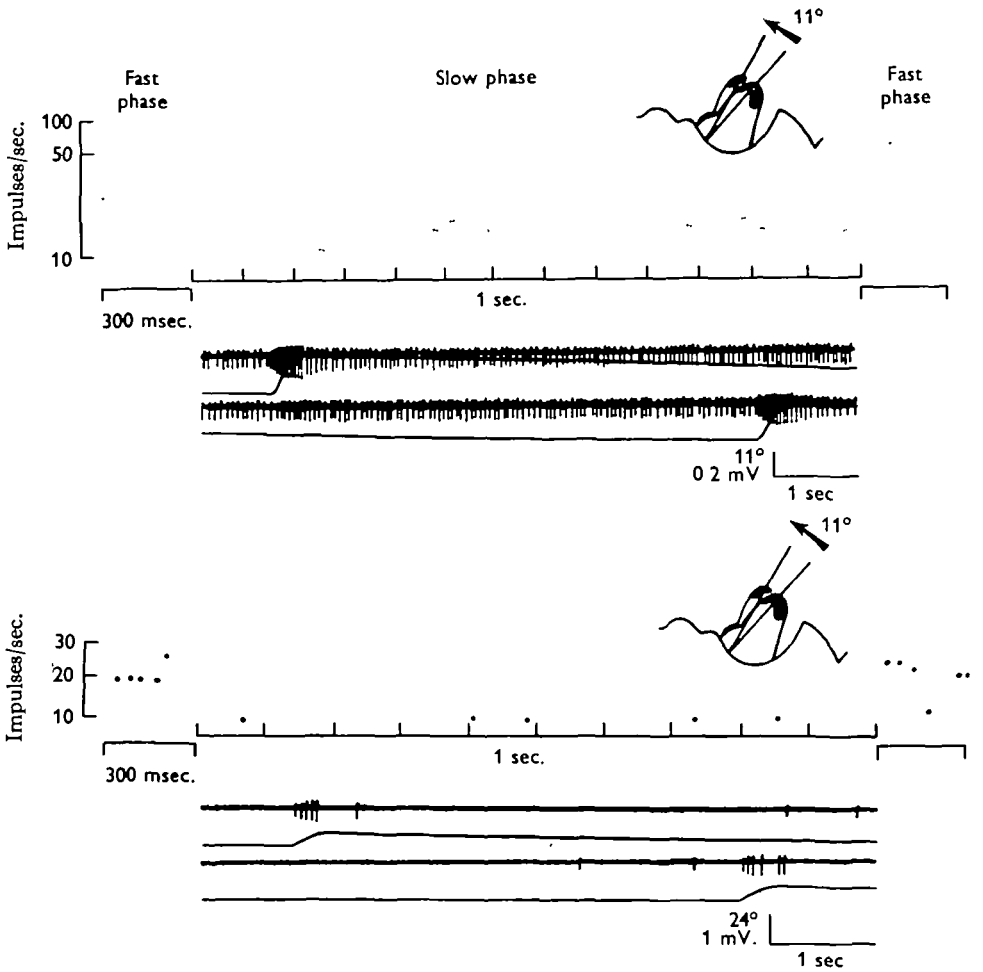

Fig. 15. Tonic (upper) and phasic (lower) activity in muscle 22 during a slow-phase movement toward the midline and a fast return phase away from the midline. No trend is apparent in the tonic activity during the slow phase, but during the fast phase the frequency is raised. There is a burst of phasic activity at a low frequency only after the start of the fast phase.

midline the frequency declines from 30 to 15 Hz. (Fig. 16). Activity then increases in amplitude and frequency to reach a peak of 60 Hz. during the fast return phase, but declines gradually once more during the next slow phase. Throughout a slow phase towards the midline a steady discharge at a frequency of 20–25 Hz. is maintained, but is inhibited centrally 100 msec. before the start of the fast phase, and suppressed for 150 msec. of this phase (Fig. 17). During the latter half of the fast phase the tonic

frequency is raised to 50 Hz., but this then declines rapidly to 20 Hz. during the next slow phase.

Phasic activity in this muscle is completely absent during a slow phase in either direction but at the beginning and end of a fast phase towards the midline there is a short burst of facilitating potentials (Fig. 16).

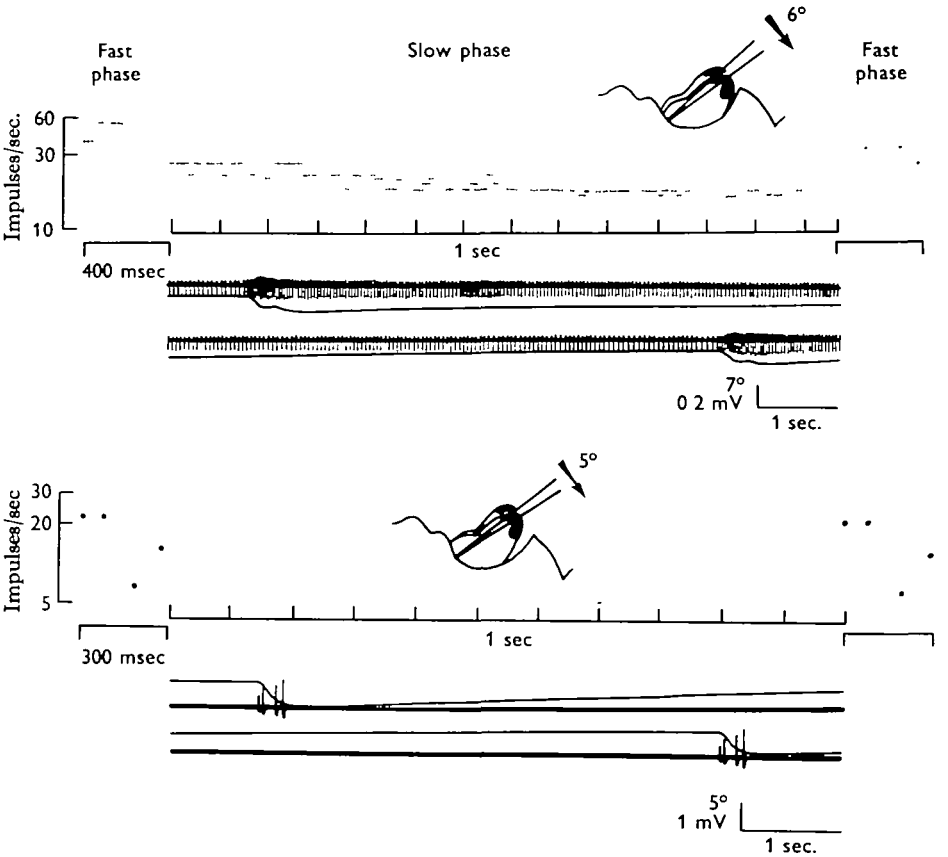

Fig. 16. Tonic (upper) and phasic (lower) activity in muscle 23a during a slow-phase movement away from the midline and a fast return phase toward the midline. Tonic activity declines gradually during the slow phase but is raised in frequency during the fast. Phasic activity is limited to two short bursts at the beginning and end of the fast phase.

Muscle 23b. No change is apparent in the irregular slow axon discharge to this muscle of about 10 Hz. during slow-phase movements in either direction (Figs. 18, 19). During a fast phase towards the midline the frequency is raised to 20–50 Hz., and correspondingly during the first half of a fast phase away from the midline the discharge is centrally inhibited. Apart from this, tonic activity is continuous in muscle 23b throughout the whole cycle in either direction.

Phasic activity occurs only as a burst of rapidly facilitating potentials at the end of a fast-phase movement away from the midline (Fig. 19). This burst usually consists of five potentials at a frequency of 20–30 Hz. at a time when the fast-phase movement is almost complete. No eyecup movement can be directly correlated with this activity which may, however, contribute towards the deceleration of fast-phase movement.

DISCUSSION

The activity of the various eyecup muscles during horizontal optokinetic movements is summarized in Fig. 20 and Tables 1 and 2. The illustrations cover the simultaneous activity of twenty motor axons in a normal response.

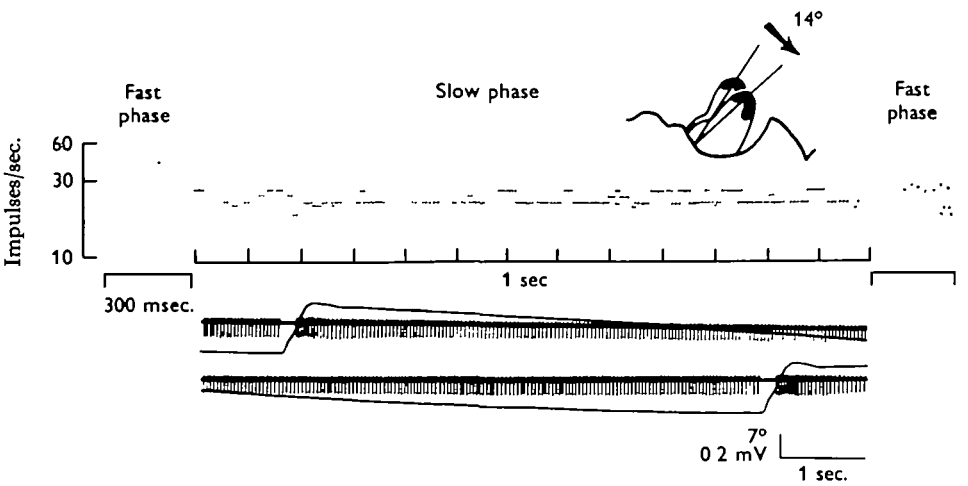

Fig. 17. Tonic activity in muscle 23a during a slow-phase movement away from the midline and a fast return phase toward the midline. The activity is relatively constant at a frequency of 25–30 Hz. during the slow phase but is inhibited centrally during the first half of the fast phase. Phasic activity is absent.

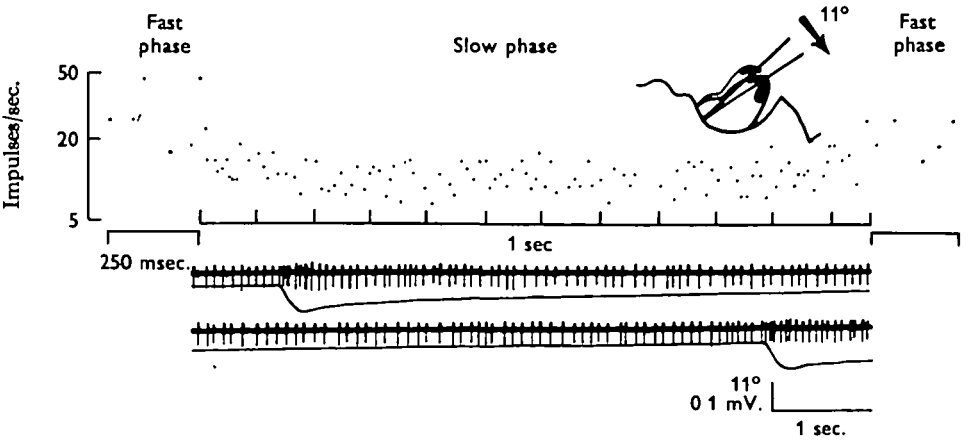

Fig. 18. Tonic activity in muscle 23b during a slow-phase movement away from the midline and a fast return phase toward the midline. The activity is irregular at 10 Hz but is raised in frequency during the fast phase. Phasic activity is absent.

Eight of the nine muscles always collaborate in their tonic activity to form the suspension system which determines the resting position of the eyecup. Muscle 19a is active only during withdrawal of the eyecup and when the eyecup is retained in its socket. In a stationary eyecup only the tonic fibres innervated by slow axons are active

(except for a few phasic fibres in muscle 21 causing horizontal tremor). Each particular efferent pattern to eight of the nine muscles corresponds to only one eyecup position.

No movement is made without a change in activity of several muscles. Slow movements are brought about by changes in the frequency of the slow axons. For larger or faster movements the phasic system is recruited. This is the situation in a slow forward phase of nystagmus. Rapid movements, such as the fast return phase of

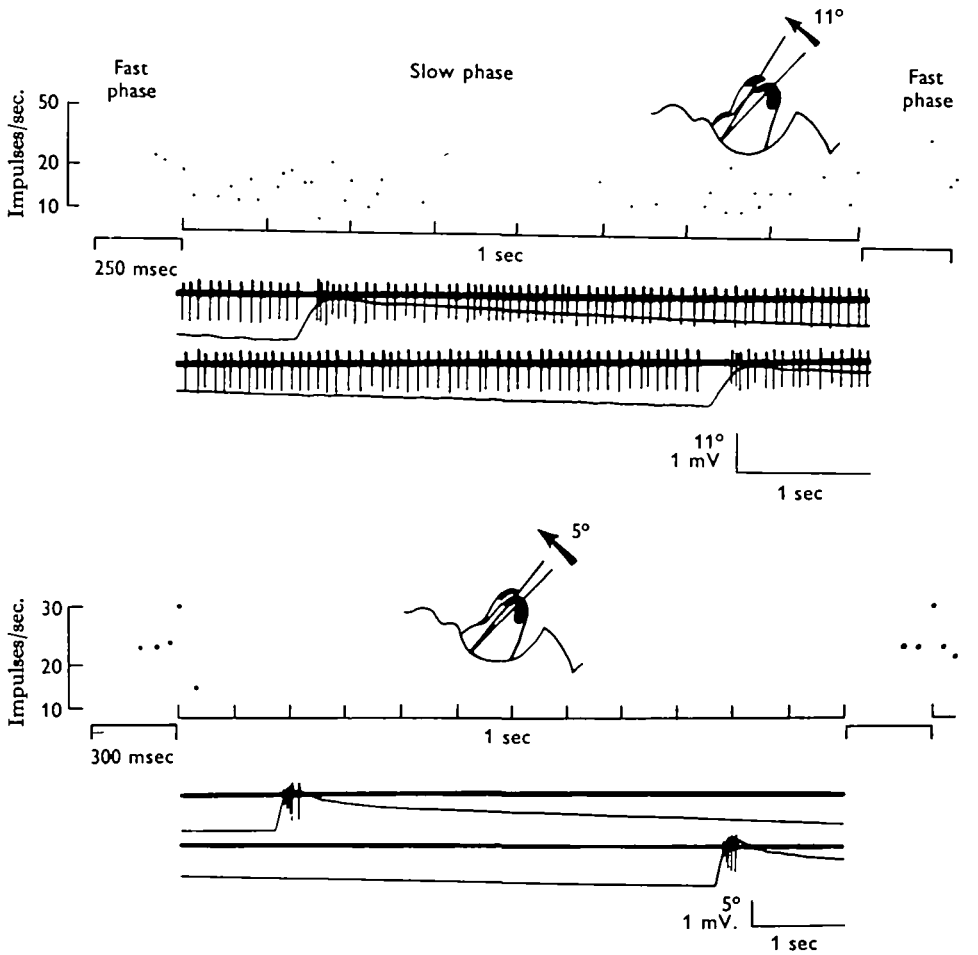

Fig. 19. Tonic (upper) and phasic (lower) activity in muscle 23 b during a slow-phase movement toward the midline and a fast return phase away from the midline. Tonic activity occurs irregularly at 10 Hz. during the slow phase but is inhibited centrally during the fast. At the end of the fast phase there is a burst of phasic activity which may decelerate this movement.

nystagmus, are brought about primarily by the phasic system, which is also responsible for tremor. Some muscles show greater activity during visually controlled movements in particular directions. Slow horizontal movement towards the midline is correlated with increased activity in muscles 21 and 19*b*, and movement away from the midline by increased activity only in muscle 20a. With other movements, however, such as the fast flick-back in optokinetic nystagmus it is difficult to demonstrate which if any of

the muscles is the chief cause of the movement, because several change their activity simultaneously. It is more correct to consider all the eyecup muscles as a group than to ascribe limited functions to individual muscles.

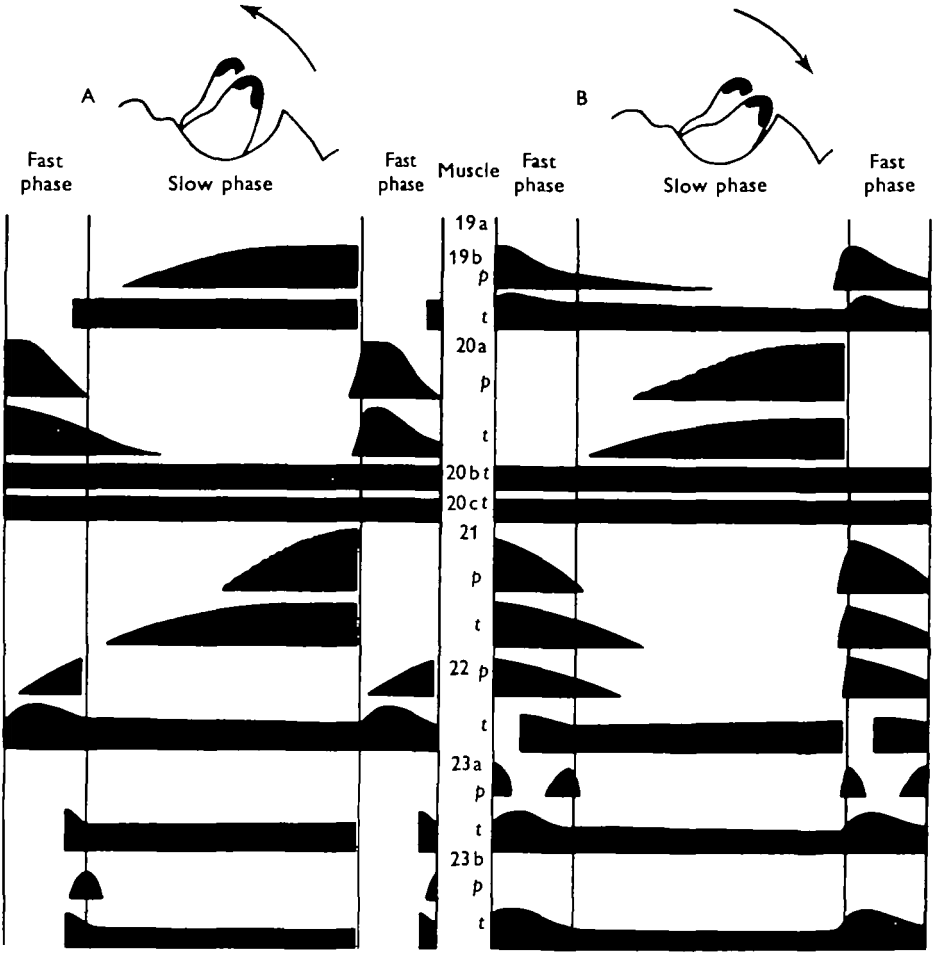

Fig. 20. Summary of eyecup muscle activity during horizontal optokinetic movements; phasic *p*, tonic *t*. In (A) the slow-phase movement is toward the midline; in (B) away from the midline. The frequency of muscle activity is represented vertically on an approximate logarithmic scale. The time scale for the fast phase is expanded relative to that for the slow phase.

Central control

The optokinetic response clearly depends on a central programme for each stimulus situation. Moreover, the programmes for opposite directions of the optokinetic response in the horizontal plane are quite different, not merely mirror images of each other. There is a remarkable constancy in the general form of the central programme of nerve impulses when the same stimuli are applied to different crabs; the principal differences between crabs lie not in the occurrence of different impulse sequences in different axons, but in the frequency of the impulses in corresponding parts of the pattern. This is in agreement with behavioural observations which show that eyecup

movements are consistent between animals, although the quantitative ratio of output to input, the velocity gain, and the region of the total possible traverse over which the nystagmus movements occur, vary over a wide range. It has been repeatedly confirmed that every position of each eyecup, and every movement, is the consequence of a patterned stream of motor impulses which depends solely upon the sensory stimulus, while the brain, in generating this pattern, is indifferent to the position or

Table 1. *Slow-phase optokinetic movement away from midline*

Muscle	Tonic	Phasic
18	Constant at 25 Hz. throughout cycle	Inactive
19a	Inactive	Inactive
19b	Declines from 20 to 15 Hz. in slow phase, but raised to 30 Hz. during fast phase	Burst at 60 Hz, 100 msec. before start of fast phase, declining during next slow phase
20a	Freq. depends on horizontal position of still eyecup. Increase to max. of 50 Hz. Inhibited centrally *before* fast phase	Inactive in still eyecup. Begins only when tonic freq. is already high. Increase to 100 Hz. Inhibited centrally before fast phase. Come in whenever eyecup moves rapidly. Patterning of potentials causes tremor
20b	Irregular at 10 Hz. throughout cycle	Irregular at 1–5 Hz. but may show a slight increase in slow phase
20c	Irregular at 10 Hz. throughout cycle	Inactive
21	Inactive in slow phase. Burst at 60 Hz. begins before onset of fast phase and declines slowly	Inactive in slow phase. Burst 200 Hz., 100 msec. before onset of fast phase and declines abruptly. Prime cause of fast phase movement
22	Increase from 10–20 to 20–25 Hz. Suppressed before fast phase and for 1st third but then resumed at 25–30 Hz.	Little activity in slow phase. Burst 200 msec. before fast phase reaching 50 Hz.
23a	Regular decrease from 30 to 15 Hz. Increase during fast phase to 60 Hz.	Inactive during slow phase. Short burst at 20–30 Hz at start and end of fast phase
23b	Irregular at 10–20 Hz. in slow phase, raised to 20–50 Hz. in fast phase	Inactive

movement of the eyecup or even to its presence. Although cuticular mechanoreceptor sensilla are present on the eyecup and are abundant in the flexible joint membrane (Sandeman, 1964), and afferent fibres in the optic tract carrying mechanoreceptive and proprioceptive information from the eyecup region are reported (Waterman & Wiersma, 1963) all experiments have failed to reveal their utilization in the immediate control of any eyecup response. A change in the speed of the visual stimulus causes an appropriate change in the rate at which the central programme appears.

Muscle structure and function

The muscles in the eyecup of the crab consist of two basic types of fibre, 'Fibrillenstruktur' and 'Felderstruktur' but intermediate types are also present. The exact correlation of the structural with the functional observations must await the marking of individual fibres after electrical recording, and their subsequent histological identification, because the various types of muscle fibres are not clearly separated anatomically as they are, for instance, in the accessory flexor muscle of the meropo-

dite of the leg (Dorai Raj & Cohen, 1964). Nevertheless, a good deal of evidence suggests adherence to the general rule found for other crustacean muscles that the fast axons supply the 'Fibrillenstruktur' fibres while the slow axons supply the 'Felderstruktur' ones. For example, in muscle 23b the tonic activity is only recorded

Table 2. *Slow-phase optokinetic movement towards midline*

Muscle	Tonic	Phasic
18	Constant at 25 Hz. throughout cycle	Inactive
19a	Inactive	Inactive
19b	Gradual increase from 15 to 20 Hz. inhibited centrally before and for 1st 100 msec. of fast phase	Gradual increase to peak of 20 Hz. midway. Maintained until inhibited centrally at start of fast phase
20a	Inactive in slow phase. Burst at 50–100 Hz. before onset of fast phase movement, declining slowly	Inactive in slow phase. Burst at 200 Hz. before onset of fast phase movement, declining abruptly. Prime cause of fast phase movement
20b	Irregular at 10 Hz. throughout cycle	Irregular, but slight decrease in slow phase and increase during fast
20c	Irregular at 10 Hz. throughout cycle	Inactive
21	Freq. depends on horizontal position of eyecup. Increases to max. of 40 Hz. Inhibited centrally before fast phase	Bursts cause eyecup tremor. Begin only when tonic freq. already high and eyecup movement half completed. Increase to 200 Hz. but inhibited centrally before fast phase. Come in whenever eyecup moves rapidly. Patterning of potentials causes tremor
22	Irregular at 10–20 Hz. raised to 50 Hz. during fast phase	Little activity in slow phase. Burst at 20 Hz. after fast phase movement has begun
23a	Constant at 20–25 Hz. Inhibited centrally before and for 1st 150 msec. of fast phase	Inactive
23b	Irregular at 10–15 Hz. Inhibited centrally before and for 1st 100 msec. of fast phase	Inactive in slow phase. Burst of five potentials at 20–30 Hz. at end of fast phase. May decelerate this movement

from the superficial fibres which are known to be the 'Felderstruktur' fibres histologically. In muscle 19b, where there are intermediates but no extreme 'Fibrillenstruktur' fibres present, the phasic activity differs from that in other muscles. The phasic junction potentials of 19b have a slower rise time, a longer time constant of decay and show little facilitation. This could be caused by the fast axon supplying the muscle fibres of intermediate type.

A feature of the detailed anatomy, as revealed by repeated probing of numerous muscle fibres in each preparation, is the diversity of the muscle fibres in a small space. Although all nine muscles occupy a region only a few cubic millimetres in extent, each muscle contains tonic and phasic fibres which merely represent the extremes of a wide spectrum of fibre types. The slow and fast motor axons are distributed in a pattern which imposes further diversity. There are twenty to thirty types of muscle fibres in the eyecup out of a total population of about 150. This diversity seems to be reasonably constant from crab to crab so far as the sampling technique with microelectrodes allows one to say; certainly the distribution of fast and slow axons is anatomically similar in all specimens.

The functional need for such diverse peripheral neuromuscular mechanisms appears to lie in the wide variety of eyecup movements, in different directions and at different speeds. With only a few motor axons to each eyecup muscle the gradation of contraction must depend more on frequency coding than on the recruitment of motor units. The existence of two muscle fibre types, phasic and tonic, provides a low-speed and a high-speed range over which the frequency code can act.

SUMMARY

1. The actions of the nine eyecup muscles of the crab during horizontal optokinetic movements are described.

2. Each muscle includes a wide spectrum of fibre types, ranging from phasic, with sarcomere lengths of 3–4 μm., through intermediate, to tonic fibres with sarcomeres of 10–12 μm. Each muscle receives at least one slow and one fast motoneuron, but no inhibitory supply. The slow axons predominantly innervate the tonic muscle fibres while the fast axons innervate the phasic ones.

3. Slow movement and the position of the eyecup in space are controlled by the frequency of slow motoneuron discharges. All muscles collaborate at every position. The phasic system is recruited during rapid eyecup movements of large amplitude.

4. In optokinetic nystagmus the exact form of the impulse sequences are described for each muscle. They are the consequence of a visually driven central programme which takes no account of the movement which it generates. Movements in opposite directions involve different central programmes; the one is not merely the reverse of the other. There is no effective proprioceptive feedback from the eyecup joint or from muscle tension receptors.

REFERENCES

ATWOOD, H. L., (1963). Differences in muscle fibre properties as a factor in 'fast' and 'slow' contraction in *Carcinus*. *Comp. Biochem. Physiol.* **10**, 17–32.

ATWOOD, H. L. (1965). Excitation and inhibition in crab muscle fibres. *Comp. Biochem. Physiol.* **16**, 409–26.

ATWOOD, H. L., HOYLE, G. & SMYTH, T. JR. (1965). Mechanical and electrical responses of single innervated crab-muscle fibres. *J. Physiol.* **180**, 449–82.

BURROWS, M. & HORRIDGE, G. A. (1968). Eye-cup withdrawal in the crab *Carcinus* and its interaction with the optokinetic response. *J. exp. Biol.* **49**, 285–97.

COCHRAN, D. M. (1935). The skeletal musculature of the blue crab, *Callinectes sapidus*, Rathbun. *Smithsonian misc. Collns* **92** (9), 1–76.

COHEN, M. J. (1963). Muscle fibres and efferent nerves in a crustacean receptor muscle. *Q. Jl microsc. Sci.* **104**, 551–9.

DORAI RAJ, B. S. & COHEN, M. J. (1964). Structural and functional correlations in crab muscle fibres. *Naturwissenschaften* **51**, 224–5.

HESS, A. (1961). The structure of slow and fast extrafusal muscle fibres in the extraocular muscles and their nerve endings in the guinea pig. *J. cell. comp. Physiol.* **58**, 63–80.

HORRIDGE, G. A. (1966*a*). Optokinetic memory in the crab, *Carcinus*. *J. exp. Biol.* **44**, 233–45.

HORRIDGE, G. A. (1966*b*). Perception of edges versus areas by the crab *Carcinus*. *J. exp. Biol.* **44**, 247–54.

HORRIDGE, G. A. & BURROWS, M. (1968). Tonic and phasic systems in parallel in the eye-cup responses of the crab *Carcinus*. *J. exp. Biol.* **49**, 269–84.

HORRIDGE, G. A. & SANDEMAN, D. C. (1964). Nervous control of the optokinetic responses in the crab *Carcinus*. *Proc. Roy. Soc.* B **161**, 216–46.

HOYLE, G. & WIERSMA, C. A. G. (1958*a*). Excitation at neuromuscular junctions in Crustacea. *J. Physiol.* **143**, 403–25.

HOYLE, G. & WIERSMA, C. A. G. (1958*b*). Inhibition at neuromuscular junctions in Crustacea. *J. Physiol.* **143**, 426–40.

KATZ, B. (1936). Neuro-muscular transmission in crabs. *J. Physiol.* **87**, 199–221.

KOIKE, Y. (1959). An observation on the speed of nystagmus. *Acta otolaryng., Stockh.* **50**, 377–90.

KRUGER, P. (1949). Die Innervation der tetanischen und tonischen Fasern der quergestreiften Skeletmuskulatur der Wirbeltiere. *Anat. Anz.* **97**, 169–75.

SANDEMAN, D. C. (1964) Functional distinction between oculomotor and optic nerves in *Carcinus* (Crustacea). *Nature, Lond.* **201**, 302–3.

SANDEMAN, D. C. (1967). The vascular circulation in the brain, optic lobes and thoracic ganglia of *Carcinus*. *Proc. Roy Soc.* B. **168**, 82–90.

SANDEMAN, D. C. (1968). A sensitive position measuring device for biological systems. *Comp. Biochem. Physiol.* **24**, 635–638.

WATERMAN, T. H. & WIERSMA, C. A. G. (1963). Electrical responses in Decapod Crustacean visual systems. *J. cell. comp. Physiol.* **61**, 1–16.