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MOTONEURONE DISCHARGES TO THE EYECUP MUSCLES OF THE CRAB *CARCINUS*

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INTRODUCTION

Reflexes which are controlled by statocysts are among the most predictable group of reflexes in many animals, and those of the crab are no exception. When a crab is tilted in the pitch or roll planes, the movement of the eyecups compensates for the change in body position (Bethe, 1897). The compensation is not complete; for instance, over a central range of 20° of tilt in the pitch plane, the angle through which the eyecup moves relative to the vertical is about $\frac{1}{10}$ of the angle moved by the body. The compensation in the roll plane is less complete; the angle moved by the eyecup being only about $\frac{2}{3}$ of that moved by the body (Horridge, 1966*b*). Over a small range the reflex serves to keep the facet rows of the compound eye almost parallel with the horizon. The significance of this is not known but possibly the relative constancy of orientation of the eyes is necessary to distinguish figures which differ only in their orientation, as in cephalopods (Boycott, 1960; Young, 1960).

The movement of the joint between the eyecup and the underlying eyestalk is controlled by nine eyecup muscles. The suspension at the joint consists of eight muscles in continual tonic activity, and a change in the pattern of this activity suffices to cause a slow movement. Phasic activity is superimposed on this to bring about fast movements. The anatomy and action of these muscles during horizontal optokinetic movements has been described in a previous paper (Burrows & Horridge, 1968*a*). The same muscles are involved in the statocyst responses. The sensory physiology of the statocyst receptors which signal geotactic stimuli is known in some detail (Cohen, 1955, 1960; Dijkgraaf, 1955, 1956*a*, *b*). For an understanding of the integrative action of the central mechanisms in controlling the geotactic response it is necessary to have a detailed knowledge of the motor outputs to the effector organ. The eyecups are in fact always involved in two responses, visual and geotactic, and occasionally a third action, eyecup withdrawal, is superimposed. This paper is concerned mainly with the action of the eyecup muscles and the discharge patterns of their motoneurones during the static compensatory responses, with the summation between the different parts of the effect or system when the two reflexes are elicited together.

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METHODS

The crab, *Carcinus maenas*, was rigidly held at the lateral edges of the carapace. The right eyecup was cemented into its socket and the eye was blinded by coating the cornea with black paint. The left eyecup was allowed to move freely and the eye could see a black and white vertically striped drum, the stripes of which subtended an angle of 10° at the eye. Possible influences from leg proprioceptors were avoided by removing all the limbs. The whole apparatus—crab, striped drum and micro-electrode recording apparatus—could be tilted in the pitch and roll planes while the visual field of the left eye was constant. The statocyst is rigidly fused to the body. In air the crab survives well under these conditions for up to 3 hr., which was the average duration of of an experiment. A small area of the exoskeleton of the right eyecup over the required muscle was opened using a high-speed dental drill, and intracellular recording electrodes were inserted into the muscle through the hole. Junction potentials recorded from muscle fibres having one slow motoneurone were fed to a pulse-shaping circuit which converted each potential to a pulse of constant size. These pulses were either recorded on magnetic tape or were fed directly into a Biomac 500 special purpose computer (Data Laboratories Ltd.) which plotted histograms of the intervals in the pulse trains. The resulting histograms were written out on an X–Y plotter.

RESULTS

Differences in fast and slow motoneurone discharges

Each of the nine eyecup muscles is known to receive at least one slow and one fast motoneurone (Burrows & Horridge, 1968*a*). During optokinetic movements the fast motoneurones are active only during eyecup movement whereas the slow motoneurones discharge when the eyecup is stationary or moving. Fast motoneurone discharges recorded in a freely moving eyecup with extracellular leads show an increased interval scatter at high frequencies. This is clearly seen when the reciprocal of each interval is plotted, giving an instantaneous frequency as was done in the previous paper for the discharge of a fast motoneurone to muscle 21 under visual stimulation (Burrows & Horridge, 1968*a*; Fig. 12). This qualitative observation was not at the time made more exact on account of the trends caused by rapid adaptation on the one hand and the changing stimulus on the other. The nature of fast or phasic activity makes it necessary to compromise between such short samples at different frequencies that the number of data points is inadequate, or such long ones that appreciable drift is included. Intracellular recordings were made from fibres of muscle 21 which were innervated by one fast axon. Histograms of intervals were constructed from many short segments of record from many slow-phase optokinetic responses. The segments were collected in groups of similar average frequency. By this treatment a large number of intervals can be collected at each average frequency and trends are reduced.

At very high or very low average frequencies the histograms are typical of discharges by single units. However, at intermediate frequencies a bimodal distribution of intervals results (Fig. 1) with peaks at 8–10 msec. and 25–30 msec., and with a trough between the two peaks at 15 msec. Examination of the actual records shows that the

bimodal feature does not arise because the records contain long continuous runs of intervals greater or smaller than 15 msec. but because the short intervals occur singly or in groups of three to four so that the discharge consists of doublets and clusters of potentials. At higher average frequencies this pattern is still visible in photographed

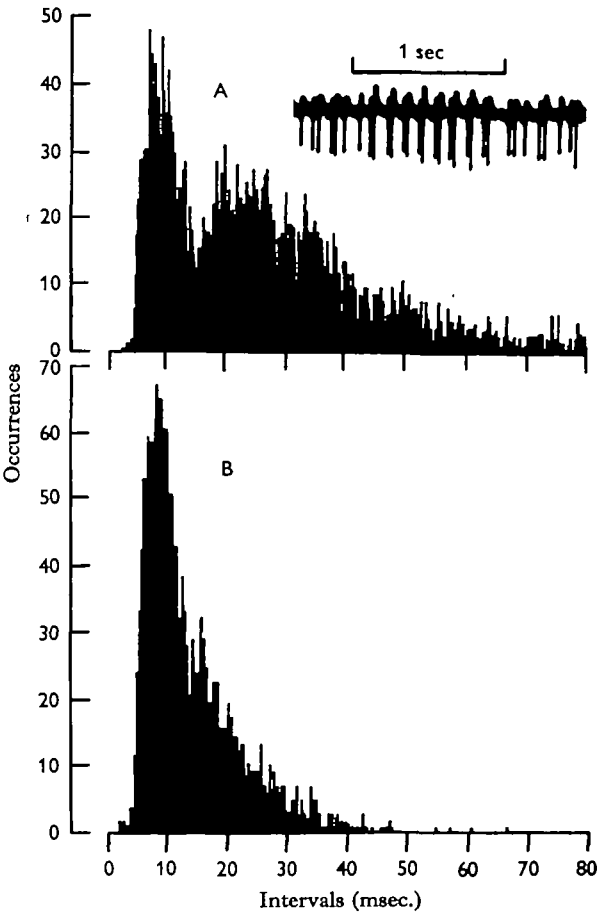

Fig. 1. Histograms of intervals for two average frequencies of fast motoneurone activity to muscle 21 of the right eyecup (open loop conditions). A. At intermediate frequencies a bimodal histogram results from the pairing of impulses, which is also shown in the extracellular muscle record (inset). B. At higher frequencies the histogram is typical of single-unit activity but patterning still occurs.

records when it no longer shows in the histogram. The pattern of the fast-motoneurone discharge is in this way similar to that described for the motoneurones to the dactyl opener (Wilson & Davis, 1965) and to the carpopodite extensor muscle of the crayfish (Atwood & Wiersma, 1967).

In contrast, the slow-axon discharge to muscle 21 (Fig. 2) or to any of the other eyecup muscles shows no pattern. These discharges are typical of most single-unit nerve impulse trains so far examined (Werner & Mountcastle, 1963; Biederman-Thorson, 1966). Low average frequencies of activity are associated with greater relative variance in interval and higher frequencies with less. This is also shown by a

narrowing of the interval histograms as the frequency increases. The fast and slow axons to the eyecup muscles thus differ fundamentally in their discharge properties, with relative variance dependent in opposite ways on the average frequency. These differences occur whether the motoneurones are driven by visual stimuli as in the previous examples or by statocyst input.

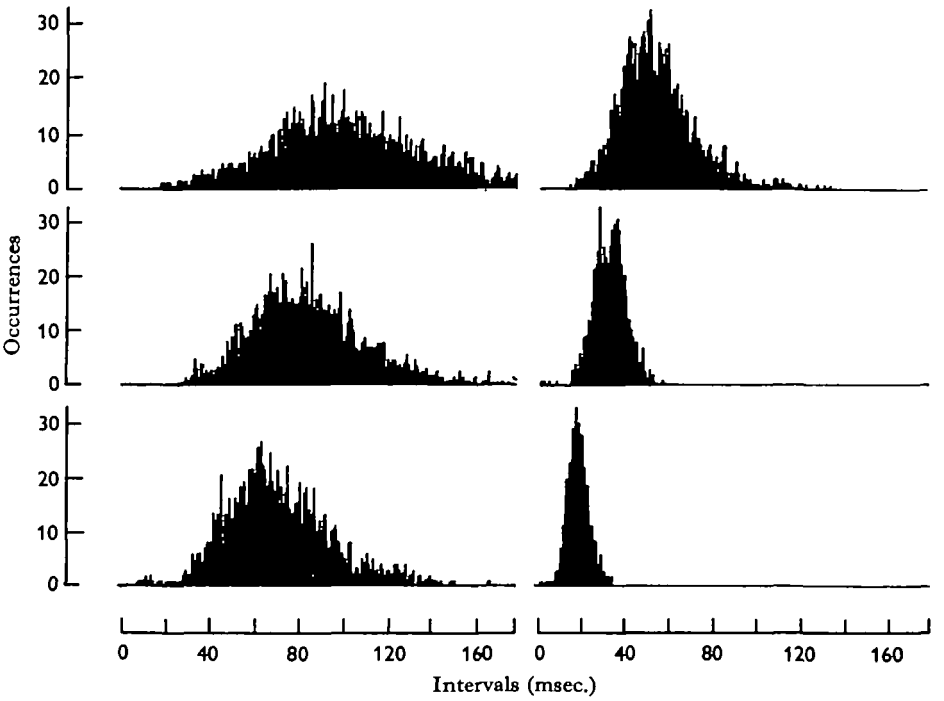

FIG. 2. Histograms of intervals in the slow-motoneurone discharge to muscle 21 at various horizontal positions of the eyecup (open loop conditions). The histograms are typical of single-unit discharges, with increased scatter at low frequencies and decreased scatter, and therefore narrower histograms, at high frequencies.

Individual muscle responses during imposed tilt

The movement of the eyecup to a new position and its maintenance there involve only the discharge of slow motoneurones when the crab is tilted slowly. Detailed data of the action of the muscles is presented in the form of histograms of intervals. Each series of histograms shows the activity of one individual slow motoneurone as recorded from one singly innervated muscle fibre at different degrees of body tilt. Hysteresis effects were checked by approaching a given position from either direction and by plotting the frequency of discharge when the crab was held horizontal at the beginning and end of each experiment. With the crab seeing a striped drum, hysteresis effects were small but increased if the contrasts were extinguished. The crab was allowed to equilibrate for 1 min. in each new position as it is known that some statocyst position receptors are sensitive to the direction of approach, but that this transient response disappears after some 30 sec. (Cohen, 1955, 1960).

Muscle 18. This is not a muscle of the eyecup joint but it causes rotation of the

eyestalk upon the carapace. During horizontal optokinetic movements the slow motoneurone to this muscle discharges at 25 Hz. irrespective of the movement of the eyecup. In roll the frequency may decline a little. However, when the anterior end of the body pitches downward to 20° below the horizontal and the eyecups compensate for the displacement by moving upwards, the frequency increases to 35 Hz. Correspondingly there is a decrease in frequency when the eyecups make a downward movement as they compensate for an upward tilt of the body. At 15° above the horizontal the frequency is reduced to 7–8 Hz. and at 20° its firing is only sporadic. The intervals are more variable at lower frequencies (Fig. 3).

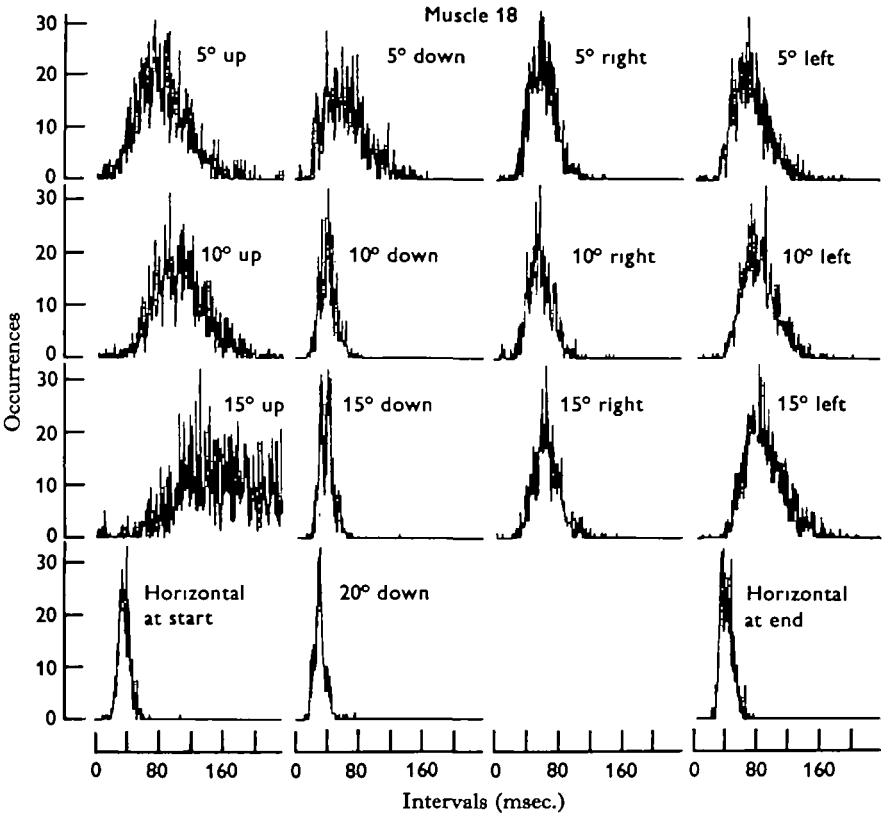

Fig. 3. Histograms of intervals in the slow-motoneurone discharge to muscle 18 of the right eyestalk. Each histogram is divided into 640 μsec. divisions so that each is the sum of more than 1000 interval counts. The histograms are arranged in vertical columns. In the first, the anterior of the crab is raised upwards in pitch; in the second it is lowered. Columns 3 and 4 show the effect of roll, i.e. tilt about the crab's longitudinal axis. In column 3 the right side of the crab moves down; in column 4 the left. A control for long-term trends is made by comparing the histograms of discharge in the horizontal position at the beginning and end of an experiment. Data for the other muscles are presented similarly.

Muscle 19a. This muscle is completely silent during all compensatory movements of the eyecup, and is active only during eyecup withdrawal movements (Burrows & Horridge, 1968*b*).

Muscle 19b. With the crab horizontal the slow motoneurone to this muscle discharges

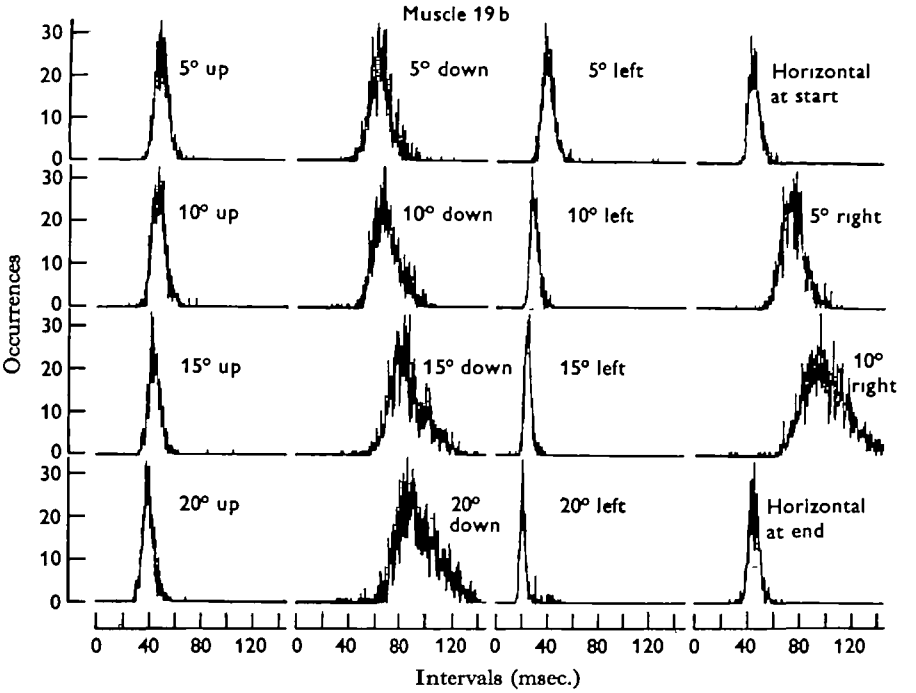

Fig. 4. Histograms of intervals of the discharge of the slow motoneurone to muscle 19b of the right eyecup during imposed tilt. The muscle shows a complex response in both roll and pitch.

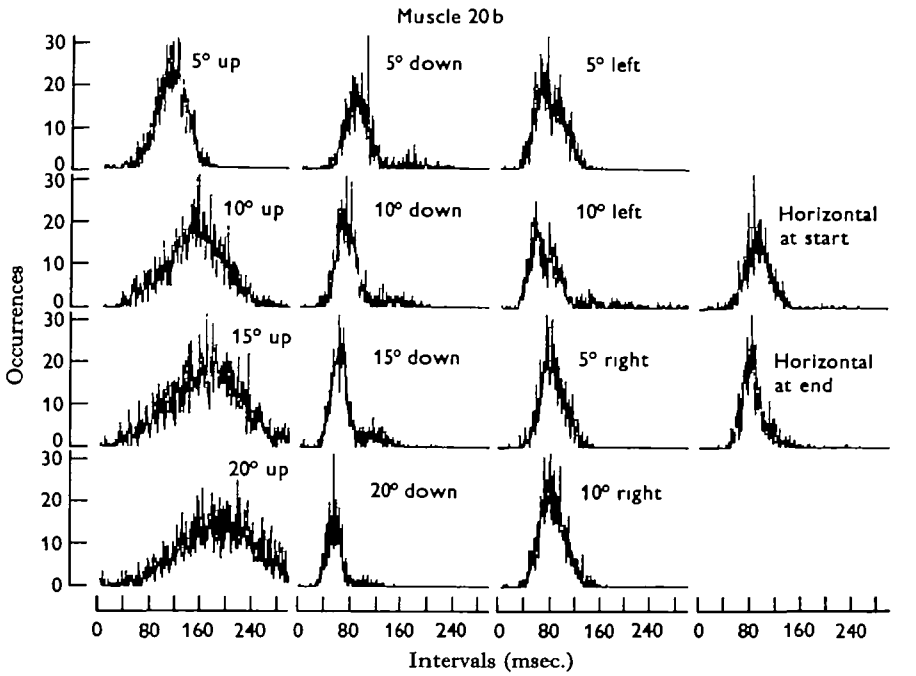

Fig. 5. Histograms of intervals for the slow-motoneurone discharge to muscle 20b of the right eyecup. The discharge is irregular at all body positions and changes only during pitch.

at 20 Hz., and is little affected by slow-phase optokinetic movements, increasing to 25 Hz. as the eyecup approaches the midline. When the anterior of the crab is pitched upwards the eyecup compensates by moving down, and the frequency increases to 25 Hz. when the crab is displaced 20° (Fig. 4). Correspondingly in downward pitch of the crab the frequency falls to 13 Hz. when the anterior is brought 20° below the horizontal. Frequency is affected to an even larger extent by roll of the body. As the right side of the animal is displaced upwards by 20° the eyecup on that side swings downwards, and the frequency drops to 10 Hz. after a 15° displacement, and to zero at a 20° displacement of the body.

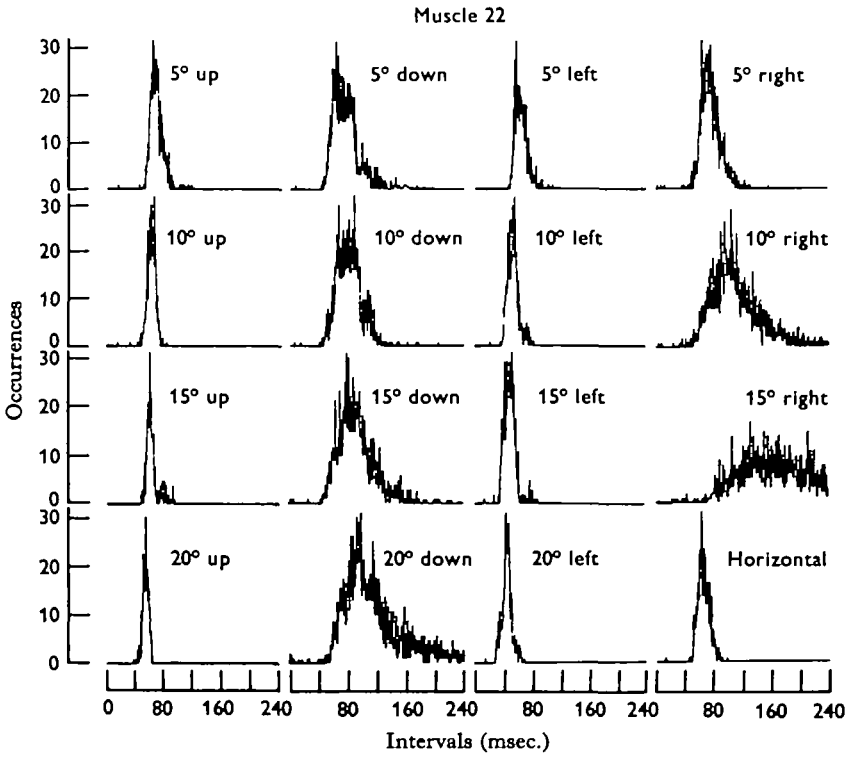

Fig. 6. Slow-motoneurone discharges to muscle 22 of the right eyecup displayed as histograms of intervals. The response of the muscle is complex, the frequency changing during both roll and pitch.

Muscles 20a and 21. These muscles are not influenced by tilt in the pitch or roll planes. The frequency of their slow motoneurones is correlated with the position of the eyecup in the horizontal plane, and they are the main muscles concerned with horizontal optokinetic movements (Burrows & Horridge, 1968*a*).

Muscle 20b. During horizontal optokinetic movements of the eyecup the slow-axon discharge continues unchanged at 10 Hz. When the eyecup compensates as the anterior of the animal is raised, the frequency declines to 5 Hz. after a 20° shift (Fig. 5). Correspondingly, when the eyecup compensates in the opposite direction, the frequency increases to 20 Hz. after a 20° displacement of the body. Roll in either direction has no affect on the frequency. In all positions of the body the intervals are irregular

as revealed by the broad histograms. Muscle 20c is also unaffected by roll but the discharge of its slow motoneurone increases in frequency to 20 Hz. as the anterior of the crab is raised, and falls to 5 Hz. as it is lowered.

Muscle 22. During horizontal optokinetic movements of the eyecup the slow motoneurone to this muscle discharges at 10–20 Hz., increasing to 25 Hz. as the eyecup approaches the lateral edge of the orbit. However, like muscle 19b, muscle 22 shows a complex response during imposed tilt, in both pitch and roll planes (Fig. 6). As the

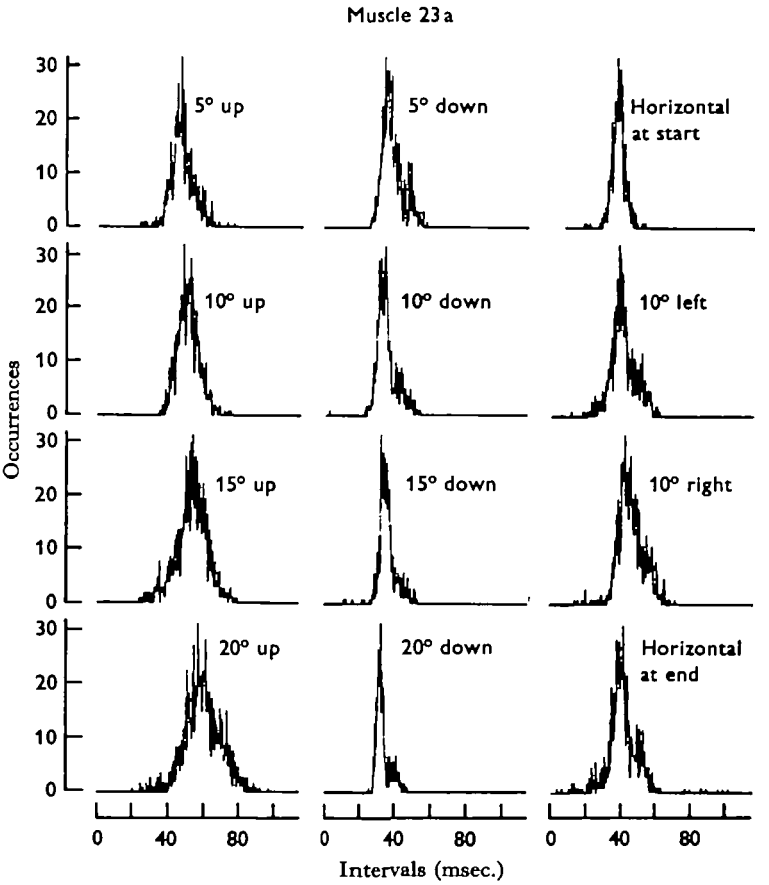

Fig. 7. Histograms of intervals of the slow-motoneurone discharge to muscle 23a of the right eyecup during imposed tilt. This muscle responds only during pitch.

eyecup is lowered when the anterior of the crab is tilted upwards, the frequency increases from 14 Hz. at the horizontal to 19 Hz. after a 20° displacement. When the eyecup is raised, the frequency falls to 10 Hz. after a 20° displacement of the body. In roll, the eyecup swings down as its side of the body moves upwards and the frequency rises to 29 Hz. after a 20° displacement. When the eyecup swings up the frequency correspondingly falls, decreasing to 9 Hz. after a 15° displacement, and then rapidly to zero for a further displacement.

Muscle 23a. During horizontal movements of the eyecup the regular slow-motoneurone discharge declines from 30 to 15 Hz. as the eyecup moves from the

medial to the lateral edge of the orbit. Tilt in the roll plane has no effect on the frequency (Fig. 7). As the anterior of the body is moved upward in pitch and the eyecups compensate by moving down, the frequency declines from 25 Hz. at the horizontal to 16 Hz. after a 20° displacement. When the eyecup is raised to compensate for a 20° downward displacement of the body, the frequency increases to 40 Hz. The extreme sensitivity of this neurone to small changes of the body position in the pitch plane is demonstrated when the tilt is applied in 1° steps. The histograms of intervals are significantly different at each position (Fig. 8).

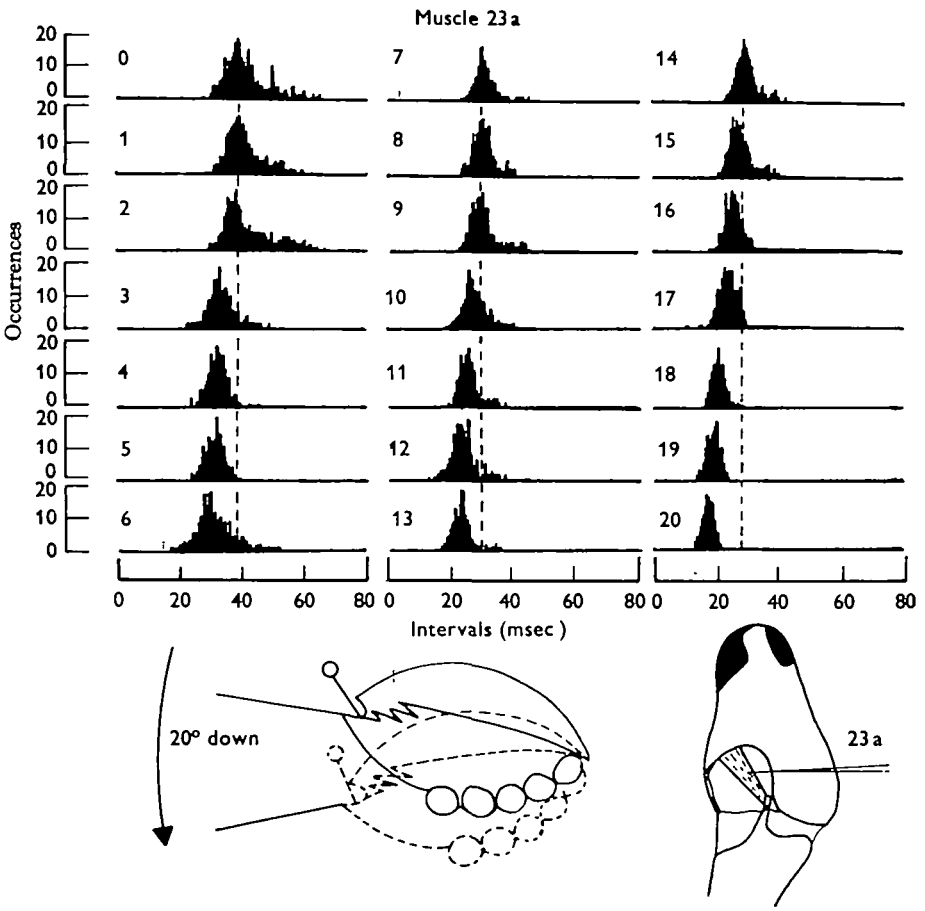

Fig. 8. The extreme sensitivity of the slow motoneurone to muscle 23a is shown when histograms are plotted for each 1° change in body position as the anterior of the body pitches downwards. A vertical line is drawn through the centre of the first histogram in each column.

Muscle 23b. Movements of the eyecup in the horizontal plane do not affect the discharge of the slow motoneurone to this muscle. However, like muscles 19b and 22, this muscle responds in a complex fashion in compensatory movements. As the eyecup moves down during an upward movement of the body in the pitch plane the frequency declines to 6 Hz. after a 20° displacement (Fig. 9). After a 20° displacement in the opposite direction the frequency increases to 12 Hz. Greater changes in frequency are

shown during roll. When the eyecup swings up as its side of the animal is lowered through 20°, the frequency rises to 30 Hz. After a 10° roll in the opposite direction, the frequency falls to 4 Hz. and eventually to zero.

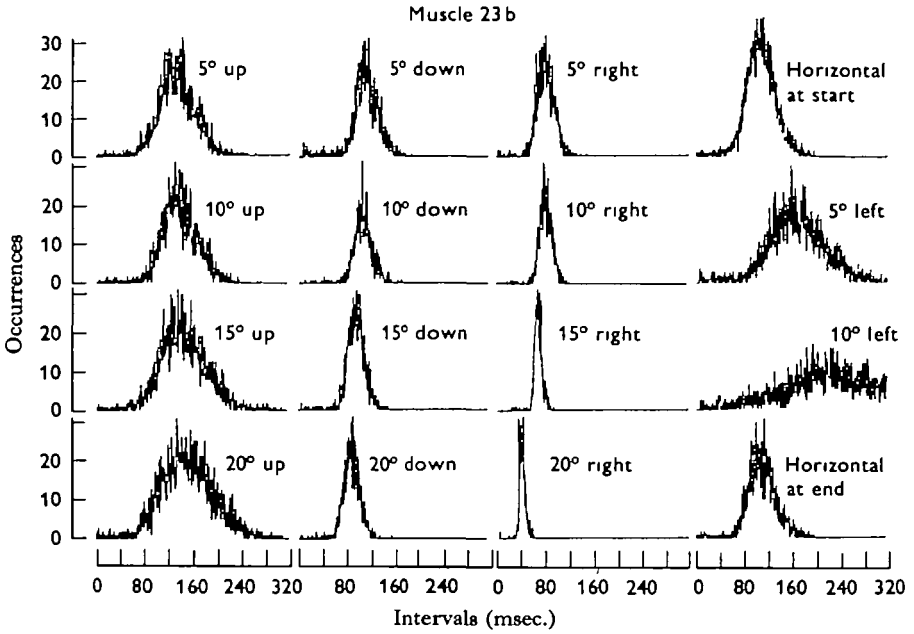

Fig. 9. The slow-motoneurone discharge to muscle 23 b of the right eyecup displayed as histograms of intervals. The response is complex, with the frequency changing in both roll and pitch.

Co-ordinated movements of the two eyecups

In horizontal or roll movements the two eyecups move in the same direction but in opposite directions relative to the midline of the crab. However, in vertical movements controlled by geotactic or visual stimuli the eyecups move in the same direction relative to the crab. Muscles 18, 20b, 23a and 23b show the greatest changes in their activity during vertical eyecup movements. As the movements of the two eyes are closely linked it might be supposed that there is a correlation in time between individual impulses to the muscles concerned.

When the delay between an impulse in one muscle and the next impulse in a second muscle is divided by the interspike interval in the first muscle, the result is called a phase histogram; it is a measure of the degree to which individual impulses to the muscles are linked (Wyman, 1965; Evoy, Kennedy & Wilson, 1967). This test of linkage was made for the slow-motoneurone discharge to muscles 20b and 23a of the right and left eyecups (Fig. 10). With this method of plotting, an impulse in muscle B which occurs midway between two impulses in muscle A has a phase of 0·5; coincident intervals have a phase value of 0·0 or 1·0 depending on which impulse is taken. At frequencies of 17·2 Hz. for muscle R20b and 18·1 Hz. for muscle L20b, which corresponded to a position of the anterior of the body 15° below the horizontal, there was no correlation between the two muscles. At frequencies of 19·1 Hz. to muscle 23a

of the right eyecup and 18·7 Hz. to that of the left eyecup, at a horizontal body position for this crab, there was again no phase linkage (Fig. 10B).

Muscles 20a and 21 are primarily concerned with movements in the horizontal plane and each muscle receives two slow axons. When the discharges of the two slow axons to muscle 20a are recorded intracellulary from two singly innervated muscle fibres, they show the same general pattern of activity during optokinetic nystagmus (Fig. 11A). Similarly, even in the stationary eyecup, small transitory changes occur together in

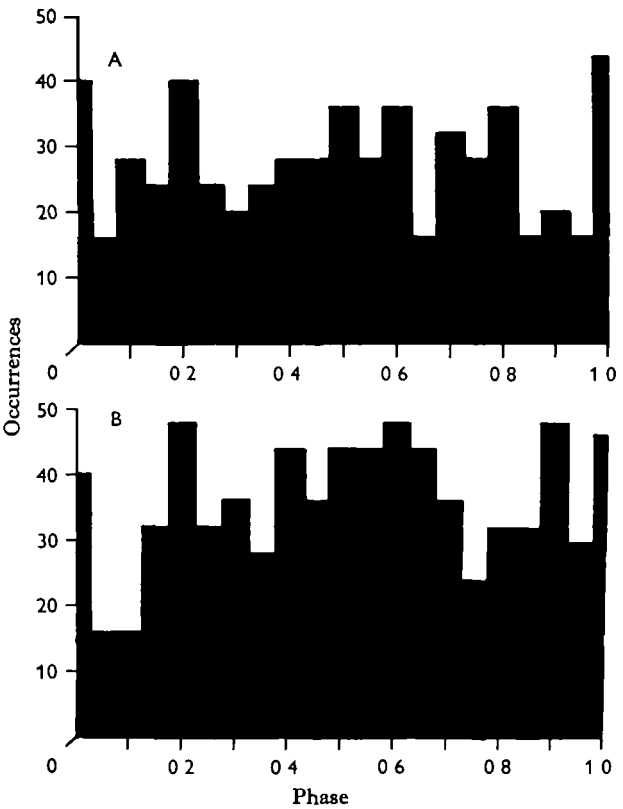

Fig. 10. Tests of phase linkage for (A) the discharges of the slow motoneurones to muscle 20b of the right and left eyecups and (B) for right and left muscles 23a. There is no close linkage between the discharge to either pair of muscles. Frequencies of discharge: (A) R20b 17·2 Hz., L20b 18·1 Hz.: (B) R23a 19·1 Hz., L23a 18·7 Hz.

both axons (Fig. 11B). A test of phase linkage of the two discharges, as defined above, with one axon firing at 19·6 Hz. and the other at 20·4 Hz., shows no relation between the timing of individual impulses in the two axons. Some fibres within muscle 20a are innervated by both slow axons and therefore show 'beats' (Fig. 11C, D) because the two axons discharge steadily at different frequencies. A similar phenomenon is reported from some leg muscles (Katz, 1936).

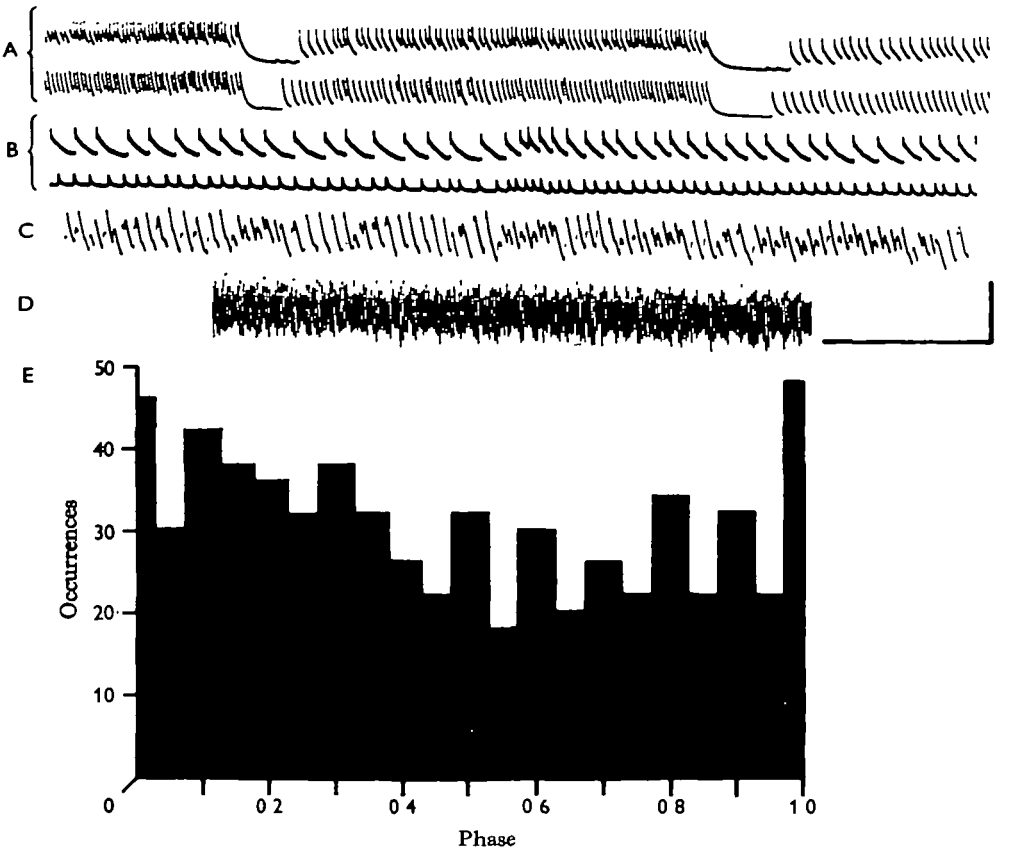

Fig. 11. Simultaneous intracellular recordings from two fibres of 20a, showing the activity of the two slow motoneurones. A. The frequency in both increases during a slow phase of optokinetic nystagmus, and both are inhibited centrally during the fast phase. B. In a stationary eyecup transitory changes of frequency are reflected in both axons. C and D. Single fibres innervated by both axons show 'beats'. E. A test of phase linkage of the two discharges with one axon firing at 19·6 Hz. and the other at 20·4 Hz. shows no interaction. Scale: Time, A,D, 2 sec. B, 1 sec. C, 400 msec. Voltage, 40 mV.

DISCUSSION

The suspension of the eyecup upon the eyestalk depends on the tonic background discharge to eight of the nine eyecup muscles and to muscle 18 in the eyestalk. The changes in these muscles when the animal is tilted are summarized in Table 1. Muscle 19a is silent, as it is also during optokinetic movements (Burrows & Horridge, 1968*a*). Muscles 20a and 21, which are the prime movers in the horizontal plane, are unaffected by imposed pitch or roll. All static positions of the eyecup are controlled by particular interactions of slow-motoneurone discharges to the remaining muscles for each position of the body. When the discharges are abolished by damage to the brain the eyecup falls limply into its socket. All movements are made by simultaneous changes of frequency in several muscles. The changes in activity during imposed tilt show that it is not possible to consider the eyecup of the crab as moved by pairs of antagonistic muscles, each pair operating in one plane alone. The only muscles that

show changes in activity during compensatory movements in a single plane are 23a and 18, and even then their action is more complex when the horizontal optokinetic movements are considered. Muscles 19b and 22 both change in slow-motoneurone frequency during both pitch and roll. Therefore separate motoneurone pathways for compensatory movements in pitch or roll plane alone do not exist in the eyecup. Similarly during optokinetic movements it was not possible to ascribe discrete functions to individual members of the same group of muscles (Burrows & Horridge, 1968*a*).

Table 1. *Frequency changes of the eyecup muscles in statocyst response*

	Pitch		Roll	
Muscle	Eyecup lowered	Eyecup raised	Eyecup swings down	Eyecup swings up
18	Decrease	Increase	—	—
19a	—	—	—	—
19b	Increase	Decrease	Increase	Decrease
20a	—	—	—	—
20b	Decrease	Increase	—	—
20c	Increase	Decrease	—	—
21	—	—	—	—
22	Increase	Decrease	Increase	Decrease
23a	Decrease	Increase	—	—
23b	Slight Decrease	Slight Increase	Decrease	Increase

— No effect

The eyecup-eyestalk joint consists of a flexible membrane that can bend in all directions because there is no hinge. It is possible that a muscle with no detectable change in impulse frequency may, nevertheless, contribute to a movement as the balance at the flexible joint is changed by the other muscles. If this is so the action of some muscles at certain times is to shorten or to resist lengthening without an impulse pattern which is related to the eyecup movement. Interpretation of changes that are seen in any one muscle has therefore to be based on the activity of the whole group.

The slow motoneurones are responsible for the control of all static eyecup positions. Successive intervals between impulses in these neurones are not known to be correlated and at high frequencies the relative interval variance (s.d./mean) decreases. In contrast, the fast-motoneurone discharges to muscles 20a and 21 have an unusually large number of pairs and closely spaced groups of impulses, which occur especially at high frequencies. This pattern is not entirely a product of the central mechanisms because the tremor of the eyecup which it causes in the horizontal plane can be modified by manipulation of the visual input. The mean interval value for the shorter intervals of the pairs or clusters is near to that found to be most effective in increasing muscle tension in other crustacean muscles (Ripley & Wiersma, 1953; Wilson & Davis, 1965). The eyecup tremor which results has a functional significance in influencing the perception of contrasting objects (Horridge, 1966*a*).

Summation of reflexes

Although optokinetic movements in the vertical plane and responses to acceleration in the horizontal plane actuated by statocyst thread hairs (Cohen, 1955, 1960; Dijkgraaf, 1956*a*, *b*) have not yet been investigated electrophysiologically, there is

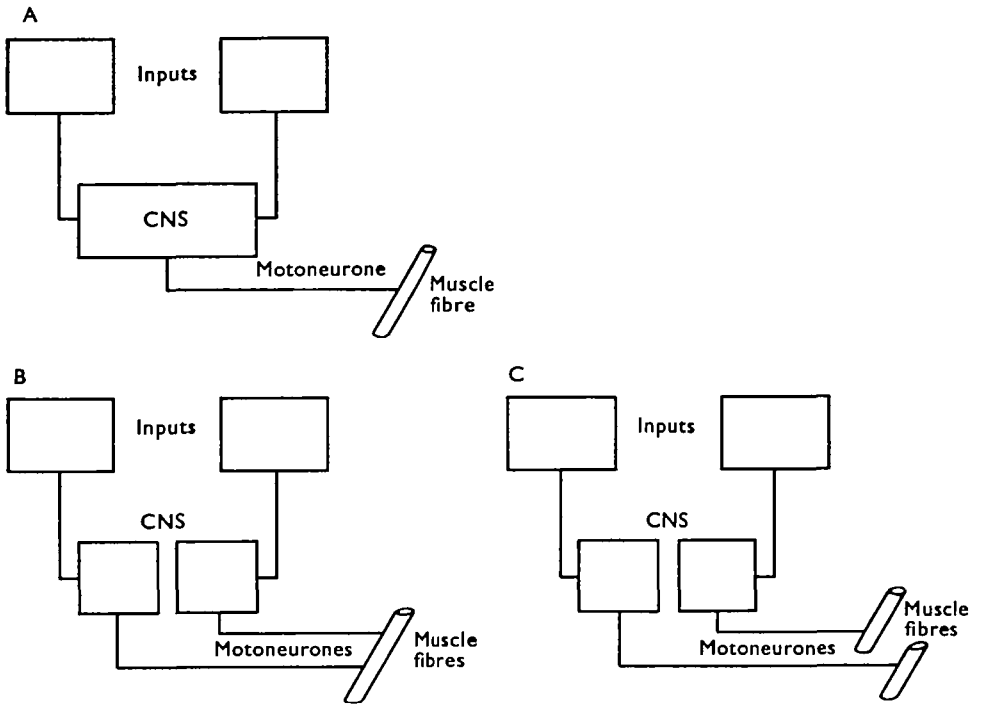

Fig. 12. Three possible ways in which separate inputs could be summed to produce integrated movements of the eyecups. A, by a common motoneurone; B, by two motoneurones to a common muscle fibre; C, by entirely separate pathways to different muscle fibres.

clearly a summation of optokinetic and geotactic reflexes. This summation could take place in at least three possible ways (Fig. 12).

1. The inputs could be summed in the brain and their outputs carried along *a common motoneurone* to the muscles. In the crab eyecup this mechanism is common in the control of tonic muscle fibres by slow motoneurones. For example, the frequency of the single slow-axon discharge to muscle 23a is influenced strongly by imposed pitch and to a lesser extent by horizontal optokinetic stimuli.

2. The inputs could remain separate within the brain and then separate motoneurones could *converge upon a single muscle fibre*. In the crab eyecup summation at the level of the muscle fibre is illustrated in the control of optokinetic and withdrawal reflexes by fast motoneurones. To muscles 20a and 21, for example, the output for these reflexes is carried by separate motoneurones which run in different nerve trunks and converge on the same muscle fibre (Burrows & Horridge, 1968*b*).

3. The inputs could remain separate within the brain and the output from each could be carried by *separate motoneurones to separate muscle fibres*. Summation then

occurs in the mechanical movement of the whole eyecup. To a large extent the phasic and tonic systems are separated in this way in the crab eyecup, and also the different muscles are integrated only in the final response. If some muscle fibres in category 2 above fail to receive innervation from either of the two axons, they will be single muscle fibres participating in a single reflex.

Movement of both eyecups

When the eyecups move in the vertical plane, driven either by the eyes or statocysts, they move together in the same direction relative to the body of the animal. Impulses to the muscles of the right and left eyecups which are primarily concerned with movement in this plane change together in average frequency but are not phase linked, as defined in the text. There is no evidence for interaction of individual impulses in different motoneurones, and even at low frequencies the linkage is less than might be expected if there were a common presynaptic input to separate motoneurones of each side. However, nothing is known of the connexions of the motoneurone dendrites beyond their location in ill-defined areas of the brain. The movement of the two eyecups is nevertheless similar, because the average frequencies to corresponding muscles are similar and partly because the tension changes are sluggish in tonic muscle fibres (Atwood & Dorai Raj, 1964; Atwood, Hoyle & Smyth, 1965) so that irregularities in the neurone discharges will be smoothed by the mechanical properties. Close linkage is therefore not essential even between two slow motoneurones to a single fibre, as that illustrated in Fig. 11 C and D for muscle 20a, which is primarily concerned with the fine control of horizontal optokinetic movements.

Some evidence has been presented that slow axons predominantly innervate tonic muscle fibres of the eyecup (Burrows & Horridge, 1968*a*); this is confirmed here, but the fibre types within a given muscle are so intermingled that a correlation between functional and anatomical observations, which is possible in some crustacean muscles where they are separated in blocks (Dorai Raj & Cohen, 1964), cannot be established in the eyecup.

If a left statocyst is removed the left eyecup still responds with a compensatory movement during imposed roll. Similarly, if a right statocyst is removed the right eyecup still responds. Therefore each statocyst affects the movement of both eyecups in the same way. In the lobster the position receptors of the statocyst are spontaneously active and in roll those on one side increase in frequency while those on the other decrease (Cohen, 1955, 1960). If either statocyst is removed, however, the resulting movements of both eyecups are unchanged. Because no other receptor types within the statocyst could provide the relevant information a 'sign-reversal' model has been invoked to explain a similar phenomenon in the control of equilibrium reactions of the abdominal appendages of lobsters (Davis, 1968). A model, similar in principle, possibly applies to the control of eyecup movements in *Carcinus*. Two different types of mechanism therefore seem likely to explain the control of the simultaneous movement of two eyecups. For optokinetic movements the opposite movements of the two eyes could depend on movement-perception fibres of opposite sense in each eye or alternatively on a central reversal mechanism. For geotactic stimuli, where either statocyst gives opposite responses and receptors of opposite sense are not known, it appears that a central reversal mechanism is essential.

SUMMARY

1. During imposed tilt the eyecup of the crab tends to preserve an absolute position which depends upon the tonic activity of eight of the nine eyecup muscles. The detailed activity of all these muscles during imposed tilt in different planes has been recorded intracellularly.

2. The slow- and fast-motoneurone discharges to the eyecup muscles differ in that the former have intervals which are more variable at lower frequencies but the latter are more variable at higher frequencies.

3. The standard deviation of the interval between impulses is 20–30% of the mean interval for a wide range of frequencies of the tonic motoneurones. This large scatter is tolerable because the slow muscle fibres are sluggish and because the eyecup is also visually stabilized by a system of long time-constant.

4. In roll the two eyecups move in opposite directions relative to the midline of the animal. In pitch the two eyecups move in the same direction relative to the body of the animal, but in neither case is there a correlation between individual impulses to the muscles of the right and left eyecups which are active at the same time.

5. Possible mechanisms of linkage between the two eyecups are discussed.

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