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TONIC AND PHASIC SYSTEMS IN PARALLEL IN THE EYECUP RESPONSES OF THE CRAB *CARCINUS*

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

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INTRODUCTION

A group of nine muscles spans the joint between the eyestalk and eyecup of the crab *Carcinus* and supports the eyecup in a complex sling. There is no simple hinge joint and the eyecup is free to move in any direction. The detailed action of these muscles has been described in the horizontal optokinetic and in geotactic responses (Burrows & Horridge, 1968*a*, *b*). Each muscle consists of a spectrum of muscle-fibre types ranging from tonic fibres innervated by typical slow motoneurones to phasic muscle fibres innervated by typical fast motoneurones. The position of the eyecup is maintained by a background discharge of appropriate frequency in each slow motoneurone. The slow motoneurones run mainly to the tonic fibres of eight muscles. Slow geotactic and optokinetic movements are brought about by changes in tonic frequency to one muscle relative to another in this system, while activity of the phasic muscle fibres is superimposed on tonic activity during sudden movements. The phasic fibres are also recruited at large displacements of the eyecup even though the eyecup velocity may be low.

One of the remarkable features is the fineness of control of the tonic eyecup movements. In experiments in which eyecup movement is the indication that the crab sees movement, the recording system must be accurate to about 0·01° in order to be better than the crab. This is all the more remarkable because each eyecup receives only some twenty motoneurones which supply muscles consisting of only 10–30 fibres. Moreover, the movement of the eyecup cannot be correlated sensibly with impulse frequency in a single muscle fibre because the position and movement of the eyecup depends on the concerted activity of all muscles in the group (Burrows & Horridge, 1968*a*, *b*). The frequencies of motor impulses and their changes are most easily measured by intracellular recording, but this technique requires that the eyecups be firmly cemented in their sockets. A direct correlation between intracellular recordings and the eyecup movement or position cannot therefore be made. However, for the visual stimuli employed, the typical eyecup movement has been recorded many times and is quite consistent from animal to animal under closed-loop conditions, that is with the eyecup free to move (Horridge, 1966*a*). Similarly the geotactic responses are remarkably consistent from crab to crab (Horridge, 1966*b*). For small slow stimuli of both kinds it is safe to assume that eyecup position changes by 85–95 % of the stimulus position. For rapid stimuli, however, the situation is quite different.

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

RESULTS

Although the present account chiefly concerns the responses of the muscles, the changes in the pattern of motor impulses depend entirely on the nature of the movements of the contrasting objects upon which the eyecups are stabilized. As a result of numerous experiments, some of which have been reported (Burrows & Horridge, 1968*a*, *b*) a number of points about the eyecup response can be clarified before the underlying electrophysiological events are described.

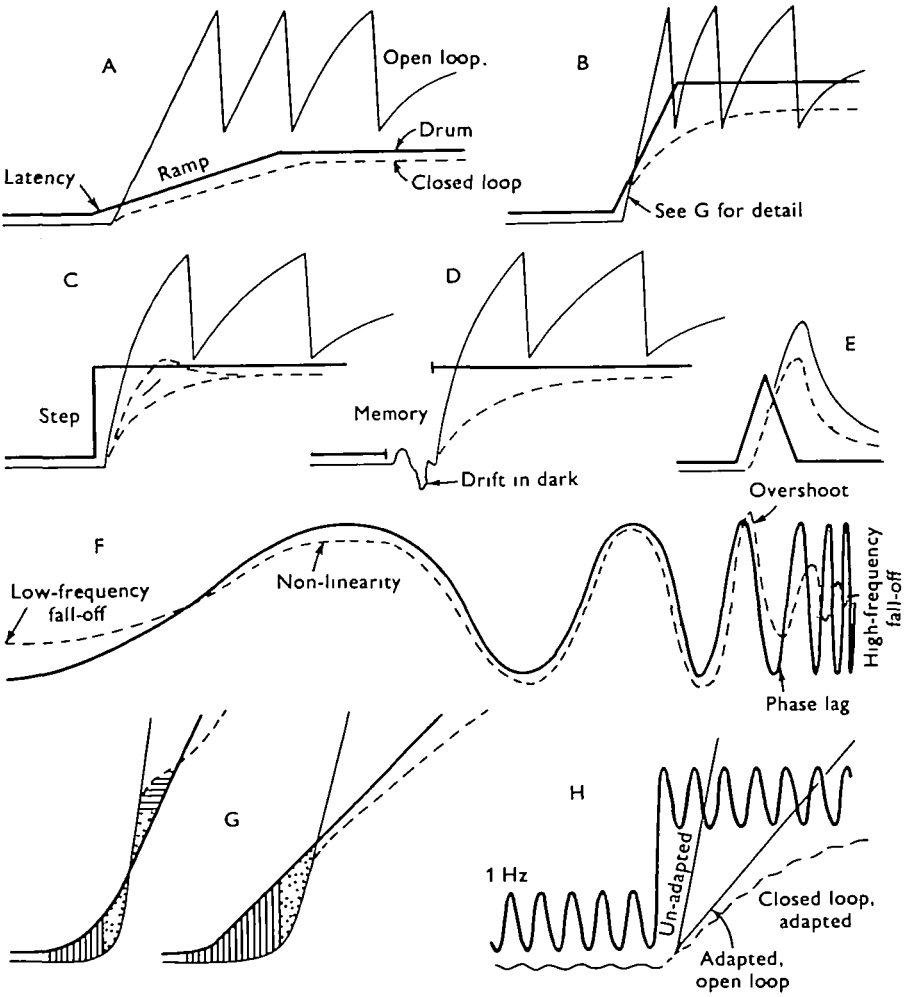

Fig. 1. Eyecup movements in response to various types of movement of all contrasting objects upon which the eye is stabilized. Closed-loop responses, dashed line; open-loop, thin line; drum movement, thick line. See text for detailed description.

The classical stimulus is the continuous rotation of a striped drum which produces nystagmus movements over about half the possible total eyecup movement. The velocity gain has been defined (Horridge & Sandeman, 1964) as the ratio of the eyecup angular speed to the stimulus speed, and the latter is the speed of the striped drum

relative to the moving eyecup. The velocity gain depends on the stimulus speed, and the remarkable feature of this amplifier is that the optimum gain is found when the stimulus speeds have low values of about 0·001°/sec. When one eyecup sees but is clamped and the response is measured as the movement of the other eyecup, which is blind, the visual feedback loop is opened and the movement of the blinded eyecup can be 10 or 20 times as fast as the movement of the stimulus across the clamped eyecup (Horridge & Sandeman, 1964). Therefore the gain can be measured indirectly with the loop closed or directly with it open, but it must be remembered that only an eyecup under closed-loop conditions is free to make its normal tremor movements of amplitude 0·05–0·2°. As will be seen, this gain is a parameter of the tonic control system and the gain of the phasic system alone is not known. A variant of this stimulus situation is the ramp function, made by starting and stopping the steady drum movement (Fig. 1 A, B). Under open-loop conditions the response, as before, is much greater than the stimulus, continues after the stimulus has stopped, and may include several traverses by the eyecup, with intervening flick-backs. Similarly, in an open-loop memory response (Horridge, 1966*a*) the eyecup movement may continue through several nystagmus movements although the seeing eyecup never actually moves at all relative to the drum while the light is on (Fig. 1 D). The most obvious difference, therefore, between the open-loop and closed-loop situations is the prolongation of the response in the former (Fig. 1 B, C).

The response to a step-function stimulus continues in closed-loop conditions only briefly after the drum has stopped because as the eyecup responds, its movement causes a relative movement of the stationary contrasting stripes across the eyecup in the opposite direction. In open-loop conditions, however, with a step-function stimulus, the movement perception of long time-constant is not cancelled, as it would be if the seeing eyecup moved, and again there is a continuation of the response, and even of fast-phase nystagmus movements, after the drum has stopped moving (Fig. 1 A, B).

The initial latency of the movement of the eyecup in closed-loop conditions means that for a time the eyecup is stationary while the drum moves. Before the eyecup starts to move, therefore, we have an open-loop situation, which causes a sudden spurt at the start of the response. For this reason the closed-loop response may even overshoot the stimulus briefly, and, with an oscillating stimulus of certain frequencies, this effect of the latency leads, for at least a few cycles, to responses of more than 100 % of the amplitude of the stimulus (Fig. 1 E–G). This temporary overshoot can also occur when the drum is given a sudden movement and held in the new position (Fig. 1 C). In the ideal case, seen at higher resolution in time (Fig. 1 G) the closed-loop response is at first zero, causing open-loop conditions (vertically hatched). Then, briefly, the eyecup moves faster than the drum (dotted region) and may overtake it. The electrophysiological analysis to follow shows that this is the period when the phasic motor system is active. In an open-loop situation, with the seeing eyecup clamped, the movement of the blind eyecup would continue at nearly this rate, but when the seeing eyecup moves, it cuts off its own response (horizontal hatching) and thereafter follows behind the stimulus.

Also relevant to electrophysiological analysis and to the subsequent consideration of the system by control theory the rate of the eyecup movement is much slower in a

response to sudden movement if the system has been habituated to a rapid oscillation for some minutes, but the total response is about the same (Fig. 1 H). This indicates that slowly and rapidly adapting movement-perception systems are separately effective in causing the optokinetic response (Horridge, 1966*c*). Finally, previous work has shown that the patterns of motor impulses which emerge from the brain and cause eyecup movements are central programmes which take no account of whether the eyecup actually moves or not (Burrows & Horridge, 1968*a*, *b*). Therefore the whole of the neural input/output relations are a feature of the supraoesophageal ganglion with no proprioceptive feedback arcs.

Oscillatory movements of the visual field

A method of studying the responses of any input/output system is to present it with small oscillations in amplitude of the input and observe the amplitude and phase lag of the response (Machin, 1964). For the crab eyecup the amplitude and frequency of the oscillations of the drum are readily controlled, the situation is convenient for conducting electrophysiology at the same time, and the results should be amenable to mathematical analysis if the response can be faithfully treated as a sinusoidal function. A supposed further advantage is that the stimulus and the response can be kept small, and the linearity of some aspects can be assumed because the eyecup is working over a small part of its range so that the fast return phase is eliminated. However, the response to the continually changing velocity during oscillations is in fact never linear because the velocity gain, defined above, depends on the angular velocity of the stimulus. Thorson (1966*a*) claims that the effect of slight unequal spacing of the striped pattern is reduced with an oscillatory stimulus. In the present work, however, the only definite advantage was that the response elicited is more consistent than that produced by continuous drum rotation.

Previous work has shown that muscles 20a and 21 have large and meaningful frequency changes which are correlated with horizontal eyecup movements (Burrows & Horridge, 1968*a*). These muscles are largely but not entirely responsible for the response in this plane.

At drum oscillations of 0·1 Hz. and amplitude of 0·15° peak to peak, the maximum frequency of the slow axon (tonic) discharge to muscle 20a of a clamped seeing eyecup shows a phase lead of 20° over drum position but at 0·5 Hz. the impulse frequency is in phase with drum position (Fig. 2). At higher frequencies of oscillation a phase lag develops, which is 20° at 1 Hz. but increases rapidly to 160° at 5 Hz. (Fig. 3). A similar relationship is found from head torque measurements in the locust (Thorson, 1966*b*) and from eyecup torque measurements in the crab *Pachygrapsus* (Sandeman, unpublished).

At the lowest frequencies of drum oscillation the eyecup begins to fail in its response by following only when the stimulus velocity is above a critical value of 3–5°/hr., so the response becomes very non-linear. At these stimulus velocities only tonic units are active. At the opposite end of the scale, as the frequency of oscillation is increased, the response does not drop out equally at all points along the chain of causation. A sinusoidal pattern of action potentials is discernible even at drum oscillations of 12 Hz., but oscillatory movement of a free eyecup ceases at frequencies of 5 Hz. Evidently the limiting feature is mechanical inertia and the eyecup is a heavily damped

system with a low resonant frequency. This is also true in the reflex postural control of the cockroach leg (Wilson, 1965), and presumably in many instances where heavy appendages are controlled. These observations imply that the time-constants of the movement-perception system cannot be calculated from the curve of response amplitude at different frequencies of oscillation at the upper or lower ends of the frequency spectrum (Reichardt, 1961), because linearity fails in one case and the movement-perception system itself is not the rate-limiting process in the other.

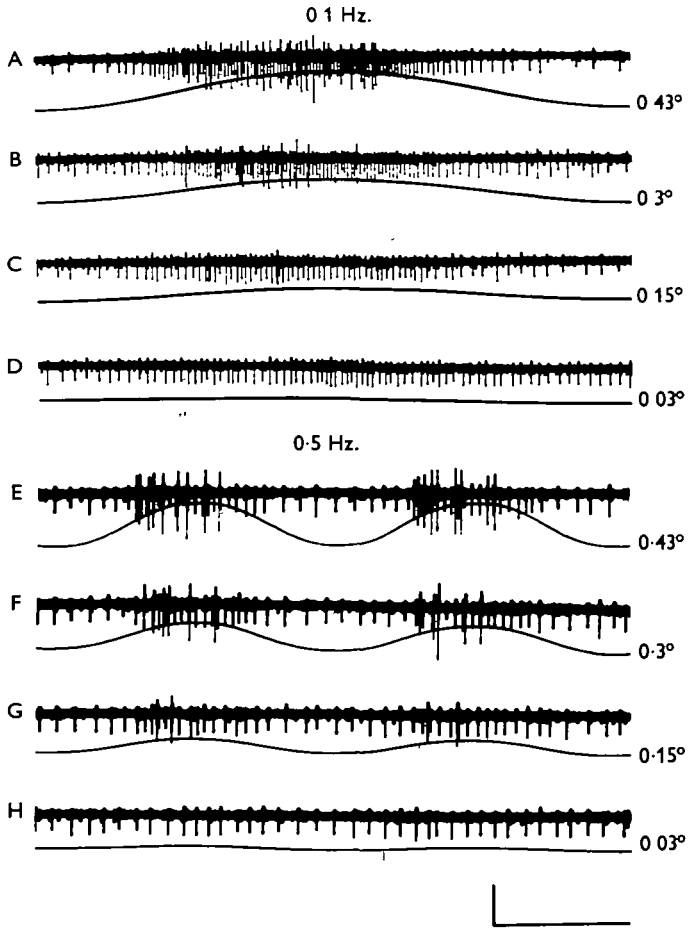

Fig. 2. Tonic (small potentials) and phasic (large potentials) activity recorded from muscle 20a of a fixed right eyecup, in response to small oscillatory movements of the drum (lower trace). The peak frequency of tonic activity shows a phase lead of 20° over drum position at oscillations of 0·1 Hz., but at 0·5 Hz. the two are in phase. Phasic activity gradually decreases as the amplitude of drum movement is decreased. Scale: voltage 1 mV.; time 2 sec. in A–D, 1 sec. in E–H.

A feature of the experiments with sinusoidal inputs is the distinction between the fast-axon and slow-axon discharges to a single muscle. The two discharges do not have the same phase relationship relative to the stimulus, but more detailed analysis has not been carried out for reasons that will be advanced in the discussion. Phasic activity is related to the amplitude of the drum movement; as the amplitude is

lowered, the phasic activity decreases and at amplitudes below 0·03° peak to peak, it is absent, although the tonic frequency changes still mirror the drum movements. If an electromechanical transducer or isometric lever is attached to a blinded, driven eyecup, an oscillatory torque can be recorded when the drum movements are so small that they cause only the tonic activity. The maximum torque exerted by the eyecup during this stimulation at small amplitude occurs at the peak frequency of tonic activity, and thus the tonic fibres alone must be capable of causing the eyecup torque during these movements.

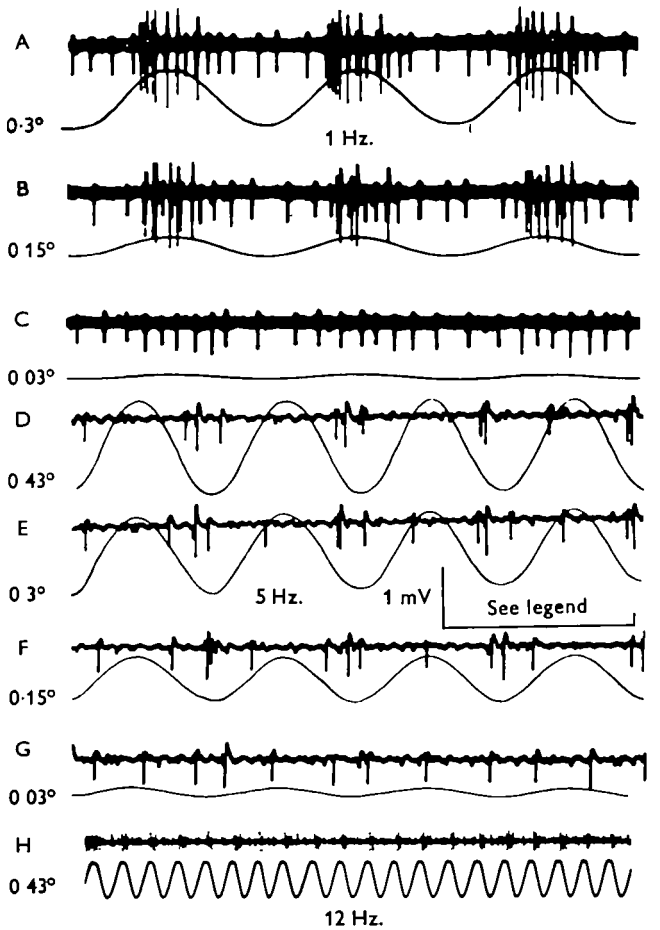

Fig. 3. Tonic (small potentials) and phasic (large potentials) recorded from muscle 20a of a fixed right eyecup, in response to small oscillatory movements of the drum. The maximum tonic frequency shows a phase lag of 20° over drum position at 1 Hz. (A–C) which increases to 160° at 5 Hz. (D–G). Oscillatory muscle activity can still be recorded at 12 Hz. (H). Time scale A–C, 1 sec.; D–G, 250 msec.; H, 750 msec. Voltage calibration, 1 mV.

Step-function visual stimuli

When the stationary drum is moved quickly through a few degrees and held in the new position, the eyecup follows the movement if free to move and slows up as it approaches its new position. The eyecup never moves through as large an angle as the drum; typically it eventually makes about 85 % of the movement of the drum.

The eyecup may take up to 2 min. to come to rest at a new position which is stabilized as before by the contrasts in the visual field. If activity is recorded from muscle 20a or 21 during this response the initial rapid movement of the eyecup is accompanied by a burst of phasic impulses, which rapidly adapt, and the subsequent follow-up by the eyecup and the new equilibrium position are caused mainly by the changes in frequency of tonic units.

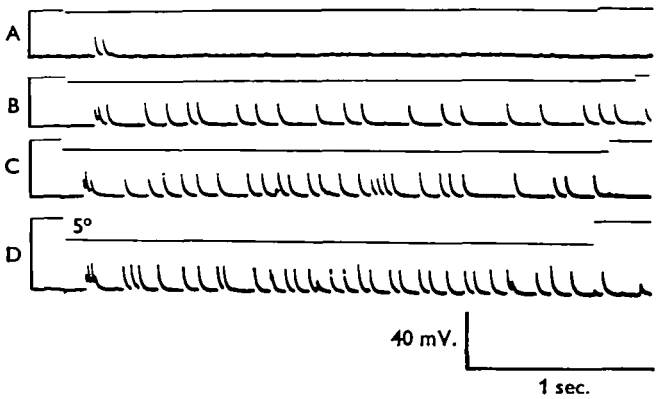

Fig. 4. Junction potentials caused by the discharge of a single fast motoneurone of muscle 21 in a clamped eyecup in response to step movements of a striped drum. With increasing displacements (A–D) of the drum from the same starting point the initial burst of activity is followed by increasing runs of activity after a decreasing delay.

For progressively larger shifts of the drum further from the same starting point the initial burst of phasic activity is followed by runs of phasic activity which increase in frequency and take longer to adapt for larger stimulus amplitudes (Fig. 4). The latency also shortens as the amplitude increases. When the eyecup is moved progressively across its traverse by successive step movements of the drum, the phasic activity which appears at each movement of the eyecup to a new position takes longer to adapt as the eyecup is deflected further each time (Fig. 5). The phasic impulses still do adapt completely after each step, however, showing that phasic impulse frequency and tonic impulse frequency are independent of each other in this stimulus situation. On account of the complexity of the response to a step function under closed-loop conditions (Fig. 1) these results were obtained with both eyecups clamped, or with both free to move, showing that the mechanisms which separately determine the frequency of both tonic and phasic impulses depend entirely on the recent history of the visual stimulus.

A familiar feature of the responses of freely moving eyecups is explained by the above results. When the contrasting objects upon which the eyecup is stabilized are suddenly moved to a new position and kept there, the eyecup response is often in two parts. First, the eyecup gives a sudden sharp response which stops quite suddenly because it is cut off by the invoked relative motion in the opposite direction. This corresponds to the end of the phasic response. Then for about 2 min. the eyecup continues to move more and more slowly as elements of long time-constant in the movement-perception system increase the frequency of the tonic motoneurones.

Numerous observations show that tonic activity is responsible for the maintenance of eyecup position after a movement. The most important group of such observations relate eyecup position directly to the whole programme of tonic motor impulses when the eyecup is held in various deflected positions by a visual or tilt stimulus (Figs. 8–10). This is true long after the phasic activity, which is temporarily seen at the shift to the new position, has adapted away.

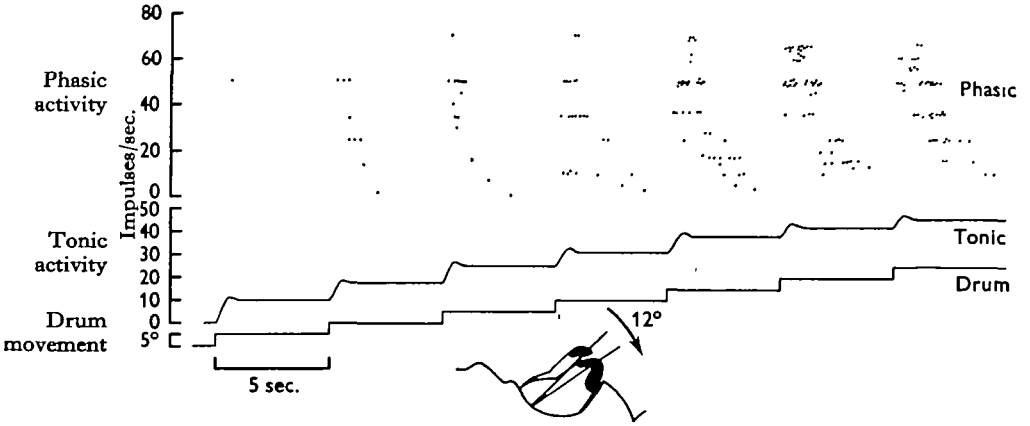

FIG. 5. Phasic and tonic activity from muscle R20a while the eyecup moves progressively across its traverse in response to successive 5° step movements of the drum. At each shift the tonic activity (plotted as a line) increases to a new level which is held constant at the new eyecup position. Phasic activity (plotted as a series of dots) increases in frequency and takes longer to adapt as the eyecup is deflected further. That it does always adapt shows that phasic impulse frequency does not depend on the tonic frequency.

Phasic fibres and tremor

Muscle 21 has the richest blood supply of any of the muscles of the eyecup and, in fact, is the only eyecup muscle with a well-developed capillary network. Groups of phasic impulses to this muscle are associated with eyecup tremor (Burrows & Horridge, 1968*a*, *b*; see also Sandeman, 1967).

When the eyecup is free to move but stabilized in one position by contrasts in the visual field, the phasic activity adapts in most of the muscles but is still recorded in muscle 21. Here bursts of potentials are associated with each movement towards the midline in horizontal tremor (Fig. 6). The bursts occur at a frequency of 2–3 Hz. and each consists of 2–20 junction potentials at frequencies approaching 100 Hz. The bursts are abolished in the dark and it is probable that they are maintained to some extent visually, being a sign of 'hunting' in the highly sensitive and rapidly adapting phasic stabilization system. Tremor of the eyecup resulting from these bursts varies in amplitude from 0·05 to 0·2° peak to peak. An angular movement of this amplitude is quite adequate to cause an optokinetic response. No comparable activity is present in the other eyecup muscles so that muscle 21, in producing tremor, must work against the passive elastic properties of the joint and the other muscles. The tremor is thus produced by an existing feature of the phasic innervation to which is added the increased blood supply to one muscle.

In all experiments, with intra- or extracellular electrodes, no phasic impulses have

been found in any muscle which could cause vertical tremor. This is negative evidence but it agrees with the finding that in two-dimensional records of eyecup movement the tremor is predominantly in the horizontal plane (Barnes & Horridge, unpublished).

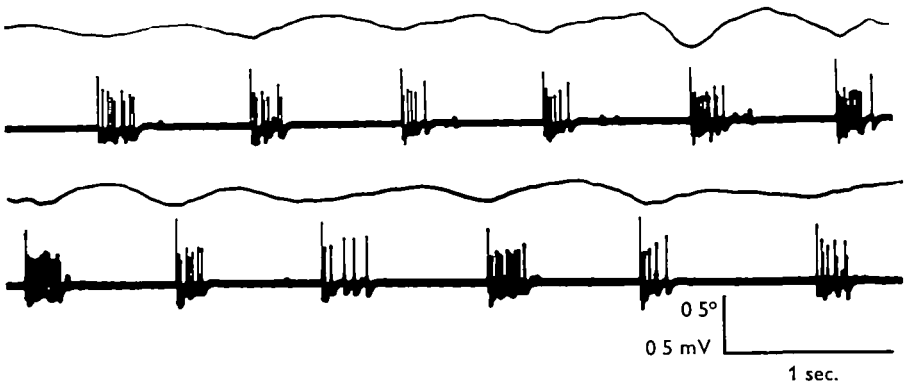

Fig. 6. Bursts of phasic activity recorded from muscle 21 while the crab was surrounded by a stationary striped drum. Associated with this activity are tremor movements of the eyecup shown on the upper trace (up is towards the midline).

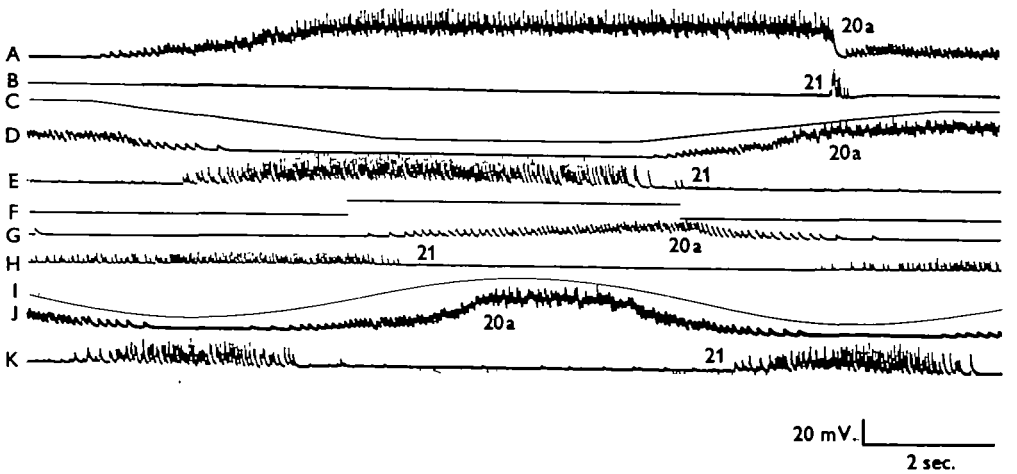

Fig. 7. Simultaneous intracellular responses of muscles 20a and 21 of the clamped right eyecup in response to some of the stimuli in Fig. 1. The fibre impaled in each muscle was supplied by a fast and a slow axon.

A and B, the response to a continuous rotation of the drum includes one complete slow forward phase and one fast phase of nystagmus. D and E, to the ramp-function stimulus shown in C (down is towards the midline) the response of one muscle declines while the other increases. Phasic impulses appear only at large stimulus amplitudes. G and H, in response to the step-function stimulus shown in F muscle 20a shows a slow increase in tonic frequency while activity in 21 is slowly suppressed. Note in *H* the long latency in the recovery of tonic activity in muscle 21. The stimulus was too small a step to arouse phasic impulses which would have appeared with short latency and rapid habituation. J and K, responses to a 0·1 Hz. oscillation of the drum, showing the reciprocal nature of the central programme to these muscles, with phasic impulses only at larger stimulus amplitudes.

Apparent antagonism between muscles 20a *and* 21

Although all positions of the eyecup are determined by an appropriate programme of activity to eight muscles, two of the muscles show an antagonism which resembles that at joints which move in only one plane. There is, however, no evidence of proprioceptive control or *reflex* antagonism between these or any of the muscles. Interference with one muscle, or with the eyecup movement, does not influence the frequency pattern of the other muscles.

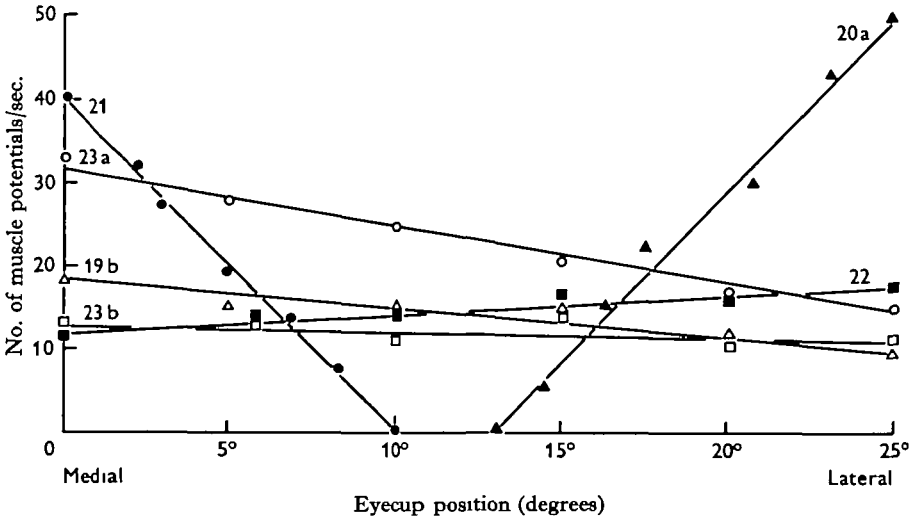

Fig. 8. Tonic muscle activity plotted against the horizontal position of the eyecup for several muscles. The eyecup was moved across its traverse by successive step movements of the striped drum, as in Fig. 5, and the average frequency of tonic activity in each muscle was measured at each position. Activity in muscle 19a is absent and that in 20b and 20c, which occurs at a constant frequency of 10–15 Hz. is omitted. Muscles 20a and 21 show the greatest frequency change during horizontal movements, and the 'preferred' position of the eyecup for this crab is in the centre of the orbit, where the activity of these two muscles is minimal.

In a slow forward phase of optokinetic nystagmus away from the midline muscle 20a progressively increases in frequency until it reaches the sharp cut off at the fast flick-back. Among many other muscles, muscle 21 is active at the fast phase, but activity begins again in 20a at a low frequency before the activity in 21 has disappeared. Similarly, with a small ramp function or oscillatory movement, or when a drum moving steadily one way is reversed, the activity of one muscle begins before that of the other has died away. A small step-function movement of the drum away from the midline causes the frequency to rise slowly in tonic fibres of 20a, while the same stimulus cuts off the activity in muscle 21, but not all at once. The drum position can sometimes be adjusted so that both 21 and 20a fire together at low background rates. Some of these features are shown in Fig. 7. In some crabs the range over which the two muscles are active does not overlap (Fig. 8). It should also be remembered that during a withdrawal of the eyecup these two muscles, each innerved by separate motoneurones, are excited together, and in concert with other muscles they then produce quite a different movement (Burrows & Horridge, 1968*c*).

Collaboration of muscles and fine control of movement

Although the eyecup muscles operate together, nevertheless, certain muscles undergo an obvious change in impulse frequency when the eyecup moves in particular directions, whereas at the same time there is little frequency change in other muscles. It is a reasonable inference, therefore, that the large changes in frequency are the principal cause of the movements which are recorded at the same time. In the antagonism between muscles 20a and 21 in the horizontal plane, the two muscles make large changes together, but one muscle increases in frequency as the other decreases

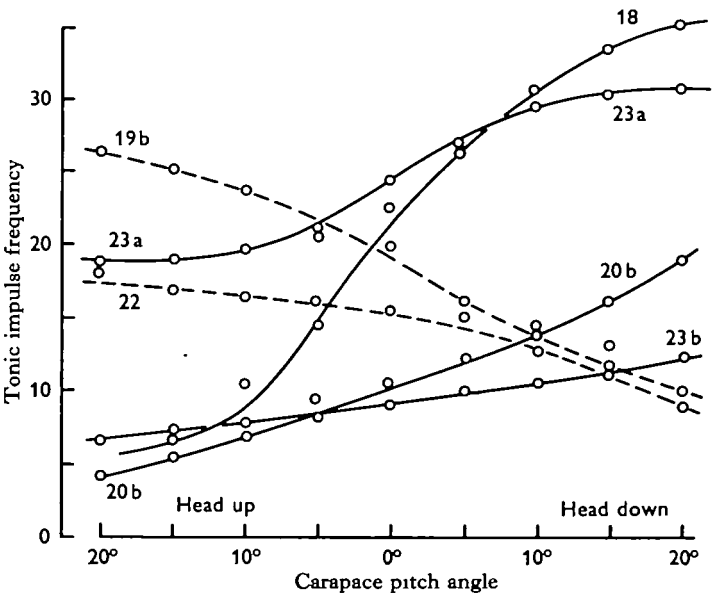

Fig. 9. Tonic motor frequencies of six muscles at different positions of imposed pitch. The four muscles 18, 20b, 23a and 23b, which increase in frequency with downward movement of the anterior of the animal, presumably raise the eyecup by counteracting gravity and the tension in other muscles. The two muscles 19b and 22 presumably act in the opposite direction, pulling the eyecup downwards. Unlike those in Fig. 10, these curves apply to both eyes simultaneously. The same data is treated by Burrows & Horridge, 1968*b*.

(Figs. 7, 8). The simultaneous changes in frequency in other muscles are much less pronounced, although they are consistent from animal to animal. In the horizontal eyecup movement it is not possible to say what twist or tilt is contributed by muscles 19b, 22 and 23b, although they certainly change their impulse frequencies as the eyecup moves. Exact details for each muscle are described in the first paper of this series (Burrows & Horridge, 1968*a*).

A different example of collaboration between muscles occurs in tilt in the pitch plane. As the crab is rotated so that the head points down, the eyes are raised mainly by increased activity in four muscles, 18, 20b, 23a and 23b (Burrows & Horridge, 1968*b*). These muscles act against the tension in the other muscles as well as against gravity. As the eyecups are raised in compensation to the above stimulus the four muscles change their frequency at different rates (Fig. 9).

Where two or more muscles collaborate one commonly shows a large change of frequency over the range of movement while the other changes over only a small frequency range. This is clearly seen during imposed roll (Fig. 10). There is, however, no question of coarse control by the one muscle and fine control by the other. The muscles are not under separate control for any given stimulus; in particular, no muscle is under proprioceptive control or can change its frequency relative to another without the appropriate change in the stimulus. The activity of the muscles is a central pattern which is not modified if the movement is prevented or if the eyecup is twisted into an abnormal position.

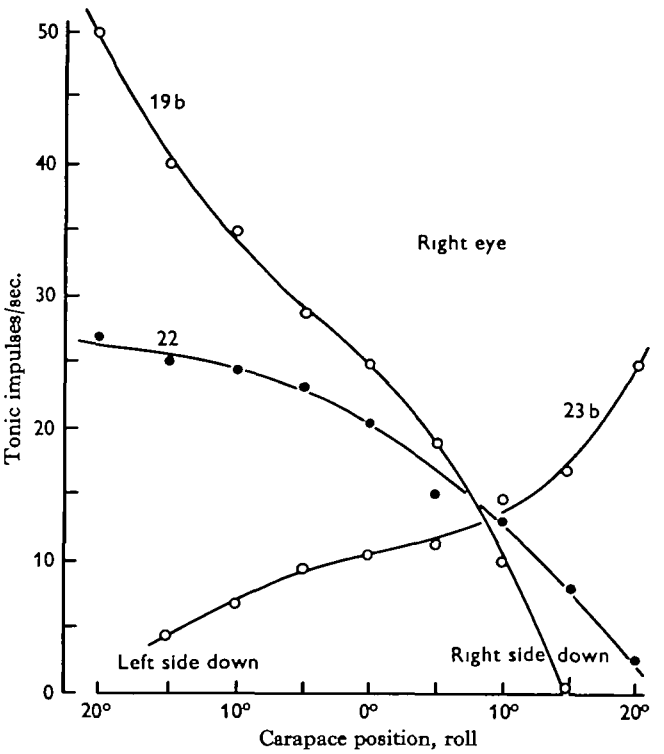

Fig. 10. An example of coarse and fine control by two muscles which act over the same range of movement. During imposed roll muscle 19b shows a large change of tonic frequency, while muscle 22 shows a smaller change. Their action is opposed by gravity and by the tension in the remaining muscles, one of which, muscle 23b, is shown here. The graphs are plotted from data treated statistically in Burrows and Horridge (1968*b*).

DISCUSSION

Tonic and Phasic systems in parallel

Optic tract fibres of the crab *Podophthalmus* that are sensitive to movement in the visual field tend to have a wide visual field, and are of several types which respond best to different speeds of movement (Waterman, Wiersma & Bush, 1964). If these movement-perception fibres cause the optokinetic responses then presumably many of them act in parallel. However, there is tonic activity of motoneurones to eight of the nine eyecup muscles when there is no movement at all in the visual field, and this is

true even in the horizontal plane for a clamped eyecup which cannot be visually stabilized. In other planes of movement the tonic statocyst responses predominate. Certainly it has not been disproved that the normal maintenance of eye position in the horizontal plane depends to some extent upon a sensory input which carries information of the actual angles subtended by contrasting objects at the eye. In all the work on crab eyecup movement, however, it has always been possible to explain the results by supposing that the brain has information only about the movement of contrasts in the visual field and not of their absolute positions (Horridge, 1966*a*). There is no equivalent of the fovea and there are no physiological markers on the retina. This is in

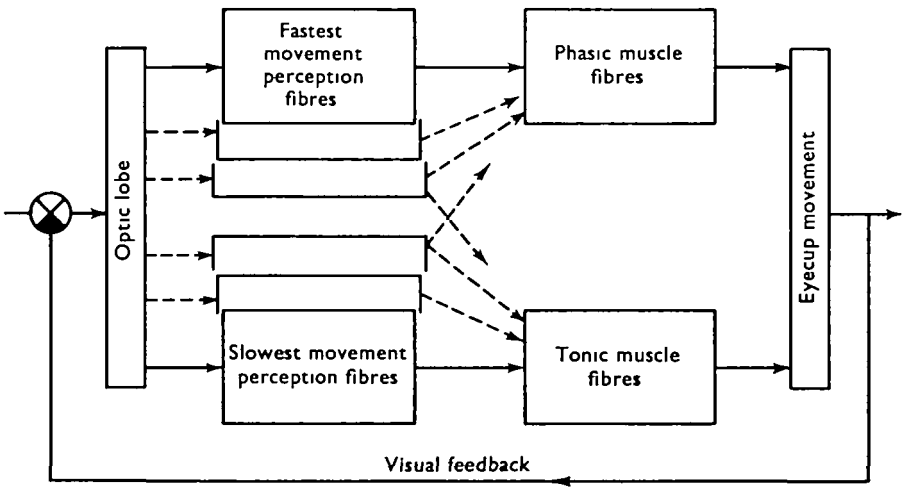

Fig. 11. Parallel pathways in the optokinetic system. The fast movement-perception system influences mainly the phasic muscle fibres while the slowest movement-perception system controls the tonic muscle fibre frequency. As indicated, there may be a spectrum of time-constants on the movement-perception side and also interaction between fast and slow systems.

agreement with the observations that no proprioceptive control of eyecup posture can be demonstrated and that the eyecup responses never compensate fully for the movement of the stimulus. Apparently the stabilization of the eyecup is entirely dependent upon detection of velocity and can be represented as in Fig. 11, with an unknown amount of interaction between tonic and phasic parallel pathways.

Support for a system of two or more parallel channels, with different time constants, comes from the behavioural observation that the eyecup response to a step function that is superimposed on an oscillation of the striped drum is slow, whereas the response to the same step function alone is rapid (Horridge, 1966*c*). As observed electrophysiologically the phasic system habituates to repeated oscillations of the drum at about 2 Hz. When the drum is now suddenly shifted to a new position, and kept there while the oscillations continue, the phasic system cannot react as it usually does. The eyecup therefore creeps slowly all the way to its new position. The normal eyecup typically responds to a sudden shift of a stationary drum by a rapid movement followed by a slower continuation that may take a minute; meanwhile the drum is stationary.

Electrophysiological analysis and control-system theory

The optokinetic system of the crab can be subjected to a sine-wave motion of the striped drum at different frequencies, or to a series of step-function stimuli, and the results could be analysed to provide a transfer function which would show the relation between input and output over the range of stimulus amplitudes and frequencies used. It might even be possible to formulate a model having the same transfer function and to calculate the time-constants of components of the model. This course was taken in the analysis of the optomotor response of *Chlorophanus*. When the experimental work on the whole animal had reached a certain stage (Hassenstein, 1958) a model of the movement-perception system was suggested and its time-constants were calculated from the overall behaviour of the intact animal (Reichardt, 1961). Quite a different procedure was adopted for the responses of the crab eyecup. The aim here has been to establish the nature of the interactions by qualitative experiments which reveal the number and placing of the components of the response mechanism. More important, the locations of the summing junctions or summation points, where loops are closed or where commands are brought in from another part of the system, have been systematically pursued by experimental manipulation.

In the response to sudden movement the rate of the eyecup movement is much slower if the system has been habituated to a rapid oscillation for some minutes. This indicates that slowly and rapidly adapting movement-perception systems are each separately effective in exciting the central eyecup optokinetic programme in the brain (Horridge, 1966*c*). The postulate of parallel fast and slow systems, which explains this, also explains the fact that in optokinetic memory experiments the response is slower after longer periods of darkness. There are no experimental results to contradict the view that rapidly adapting movement-perception systems mobilize phasic muscle systems and cause rapid eyecup movements, while slowly adapting movement-perception systems in parallel make correlations between one drum position and another over longer spans of time and excite mainly the tonic muscle systems. Each parallel pathway can have its own gain and phase relations and limits of linearity. The existence of parallel pathways, however, means that a mathematical analysis of the overall response of the intact animal, however exact the stimuli, leads to no conclusions which are relevant to the components which are clearly present and which can be confirmed by electrophysiological analysis.

Electrophysiological analysis allows an entry into the system which undermines the importance of control-system analysis upon the whole animal; it is significant that the success of the latter has been most marked for the control of the human eye, where electrophysiology is impossible (Fender, 1964). But when the actual components, such as motor impulse frequencies, have been revealed, as has been done for the crab eyecup, and the flow diagram of their interactions has been drawn, with summing points located, it is then possible to quantify each interaction. However, it is as well to question the object of such an exercise for the units of the crab eyecup. When the crab makes an optokinetic or geotactic response a very large number of different axons with different characters are excited on the afferent side; about forty different motor axons (about ten fast and ten slow to each eyecup) are excited in concert in definite patterns on the efferent side. These axons then supply eighteen eyecup muscles each

of which consists of a spectrum of muscle-fibre types, each of which in turn are probably unique in their ultrastructure and membrane properties. The activity of a single axon is meaningless in isolation. It would require a large-scale analysis indeed to reveal the motion of the crab eyecup as quantitative consequence of the transfer functions of its separate components.

Accuracy based on smoothing over a period

Both tonic and phasic fibres contribute to all responses which include, and usually begin with, a sudden movement, but the *final* position of the eyecup as it comes to rest in relation to the *final* position of the stimulus is entirely a result of the tonic system. As time elapses after the stimulus comes to a halt the eyecup is driven by components of longer and longer time-constant. In a crab with one seeing eye the eyecup can be held briefly during a stimulus and released sometime later. The eyecup then moves slowly to its new position. Alternatively, in a free eyecup the initial response of the phasic system can cause an overshoot of the final position which is then recovered by the tonic fibres. Accuracy of eyecup movement is therefore independent of the rather irregular phasic discharges.

The astonishing accuracy of eyecup movement is determined by two features of the whole tonic system which compensate for variability of the components. First, the high value of the velocity gain (from 20 to 50 for low stimulus velocities) assures a close following of the stimulus by the eye. For example, at a velocity which gives a gain of 29 the eyecup makes 29/30 of the movement of the stimulus. Secondly, the standard deviation of the intervals between tonic impulses (under open-loop conditions) of muscles 20a and 21 (which operate in the horizontal plane) is 25–30 % of the mean interval. In closed-loop conditions this gives rise to small irregular movements which cause the eye to oscillate about the desired position, although the average frequency of slow motor impulses is controlled predictably and smoothly over a wide range. The efferent irregularity necessarily contributes to the visual input. However, the long period of minutes over which the movement-perception system is able to make an autocorrelation (Horridge, 1966*a*) ensures that the response is smoothed over the irregularities in efferent impulse trains as well as the consequent irregularities in afferent impulse trains. The extraordinary accuracy of eyecup movement to about 1 min. of arc is therefore a consequence of two understandable factors, smoothing over long periods and negative feedback with high forward gain both of which are typical of artificial systems.

SUMMARY

1. Static positions of the eyecup are maintained by control of the frequency of impulses to tonic muscle fibres.

2. In addition, phasic muscle fibres are excited when an optokinetic stimulus containing frequency components faster than about 0·1 Hz. exceeds about 0·1° in amplitude.

3. Within the above limit, components of the stimulus of greater frequency or amplitude excite the phasic system, which adapts in a few seconds. Normally the tonic and phasic systems act in parallel.

4. With oscillatory movements of a striped drum the tonic and phasic units do not have the same phase relation to the stimulus.

5. The numerous components in parallel are so varied and interact at all stages, so that they cannot be related quantitatively to an analysis of the overall response.

6. Although changes in frequency at each movement are large in one muscle and small in another, there is no question of coarse and fine control because none are separately controlled or dependent on the eyecup position.

REFERENCES

BURROWS, M. & HORRIDGE, G. A. (1968*a*). The action of the eyecup muscles of the crab, *Carcinus* during optokinetic movements. *J. exp. Biol.* **49**, 223–50.

BURROWS, M. & HORRIDGE, G. A. (1968*b*). Motoneurone discharges to the eyecup muscles of the crab *Carcinus*. *J. exp. Biol.* **49**, 251–67.

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

FENDER, D. H. (1964). The eye movement control system: evolution of a model, pp. 306–24. In *Neural Theory and Modeling*, ed. Reiss, R. S. Stanford University Press.

HASSENSTEIN, B. (1958). Über die Wahrnehmung der Bewegung von Figuren und unregelmässigen Helligkeitsmustern. *Z. vergl. Physiol.* **40**, 556–92.

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

HORRIDGE, G. A. (1966*b*). Direct response of the crab *Carcinus* to the movement of the sun. *J. exp. Biol.* **44**, 275–83.

HORRIDGE, G. A. (1966*c*). Adaptation and other phenomena in the optokinetic response of the crab *Carcinus*. *J. exp. Biol.* **44**, 285–95.

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

MACHIN, K. E. (1964). Feedback theory and its application to biological systems. *Symp. Soc. exp. Biol.* **18**, 421–46.

REICHARDT, W. (1961). Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In *Sensory Communication*, pp. 303–17. Ed. W. A. Rosenblith. New York, London: John Wiley.

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

THORSON, J. (1966*a*). Small-signal analysis of a visual reflex in the locust. I. Input parameters. *Kybernetik* **3**, 41–53.

THORSON, J. (1966*b*). Small-signal analysis of a visual reflex in the locust. II. Frequency dependence. *Kybernetik* **3**, 53–66.

WATERMAN, T. H., WIERSMA, C. A. G. & BUSH, B. M. H. (1964). Afferent visual responses in the optic nerve of the crab, *Podophthalmus*. *J. cell. comp. Physiol.* **63**, 135–55.

WILSON, D. M. (1965). Proprioceptive leg reflexes in cockroaches. *J. exp. Biol.* **43**, 397–409.