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CONTROL OF HEAD MOVEMENT IN THE LOCUST, *SCHISTOCERCA GREGARIA*

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INTRODUCTION

During the last few years there has been considerable interest in the generation of patterned motor output by the central nervous system, and in the extent to which the generation of that output depends on sensory and proprioceptive monitoring of the resultant movement. This paper examines the movement control system of the head of the locust and the extent to which the motor output patterns mediating head movement are determined independent of proprioceptive feedback from sense organs monitoring head position and movement.

The neuromuscular system of the locust neck is complex and consists of 14 muscles on each side (Fig. 1) innervated by about 60 different axons originating in the suboesophageal, prothoracic and mesothoracic ganglia, and there are several proprioceptive sense organs which may be involved in monitoring head movement or position (Shepheard, 1973). Like many animals, including man, a locust moves its head in response to a relative movement of the visual field and this response which is termed 'optokinetic nystagmus' can be elicited in the laboratory by horizontal rotation of a black and white, vertically striped drum around the animal. Head movement occurs in response to a wide range of drum speeds down to less than 1°/min. This is a valuable preparation since the population of motor neurones mediating a defined piece of behaviour can be driven by the experimenter (by striped drum rotation) while the activity of single motor neurones can be simultaneously monitored by intracellular electrodes in single fibres of muscles moving the head. The system offers an excellent opportunity for study of the fine control of insect skeletal muscle and the co-ordination of motor output mediating a complex behavioural response.

MATERIALS AND METHODS

Experiments were performed on mature adult male locusts (*Schistocerca gregaria*) between 1 and 2 weeks after emerging.

Intracellular muscle recordings during head movement were obtained in the following way. The locust was mounted by its thorax above the centre of a vertically striped drum (pairs of black and white stripes subtending 18° at the eye), and head movements in the form of slow and fast phases of nystagmus were elicited by horizontal drum rotation. During optokinetic nystagmus, intracellular recordings were obtained from single muscle fibres of muscles moving the head using firmly held

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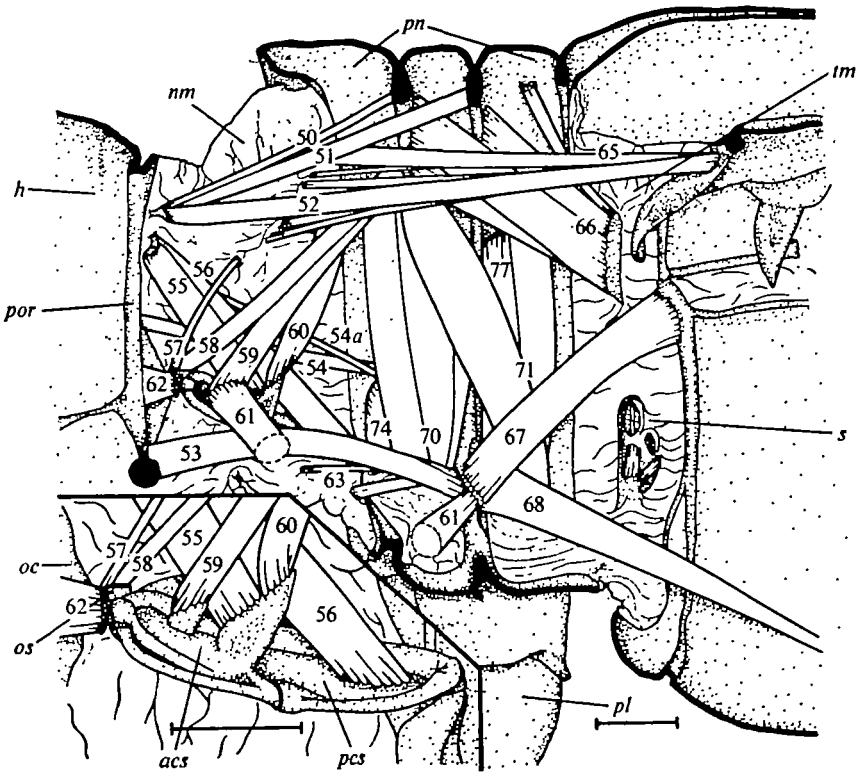

Fig. 1. The neck and prothorax of the locust in parasagittal section. Inset shows the lateral cervical sclerites in detail. *acs*, Anterior lateral cervical sclerite; *h*, head; *nm*, neck membrane; *oc*, occipital condyle; *os*, occipital cervical sclerite; *pcs*, posterior lateral cervical sclerite; *pl*, prothoracic leg; *pn*, pronotum; *por*, postoccipital ridge; *s*, spiracle; *tm*, pro-mesothoracic membrane. Scales equal 1 mm.

2·8 M-KCl-filled glass microelectrodes. Movement artifact was avoided even during quite violent muscle contractions by entering fibres close to their posterior attachment on the prothoracic cuticle, appropriate apertures being cut in the cuticle to allow access to each muscle. Using two microelectrodes, the first electrode in one fibre was used as a 'reference' electrode, whilst the innervation fields of the motor axons innervating this fibre were investigated by checking with the second microelectrode for synchrony of postsynaptic potentials (PSPs) in other fibres of the same or a neighbouring muscle. Access to some muscles is quite easily obtained. Thus muscles 50, 51, 54, 58, 59 and 60 can be reached simply by removing a small piece of the cuticle overlying their posterior insertions. Access to muscles 52 and 65 requires removal of the posterior extension of the pronotum as well as some of the meso-metathoracic membrane. The posterior insertions of muscles 53 and 61 can be reached only after removal of most of the posterior dorsal thorax (Fig. 1) and this unavoidably involves cutting muscles 52 and 65. No means were devised for recording intracellularly from muscles 55, 56, 57, 62 or 63 during optokinetic nystagmus. In many experiments, where the extent of dissection was minimal, no saline solution was used. Other preparations were perfused with saline (Hoyle, 1953) as required. Head movement was measured by a pair of photocells, an opaque flag attached to the head of the locust casting a shadow from a

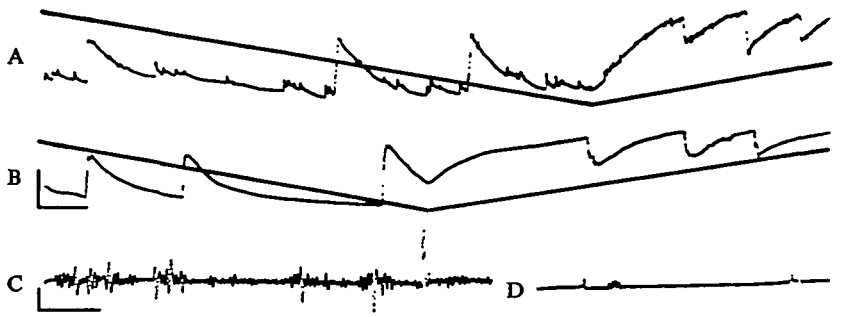

Fig. 2. The typical form of optokinetic nystagmus. In A and B the head of the locust responds with slow and fast phases of nystagmus to continuous rotation of the striped drum in the visual field (drum speed 0·6°/sec). The directions of the slow and fast phases are reversed when the direction of drum movement (indicated by ramps) is reversed. In C and D the head movement trace is a.c. coupled at higher amplification to show the faster components. Head tremor and other irregularities in the head movement of the intact animal (A and C) are largely absent after removal of the second thoracic ganglion (B and D). Vertical scales equal 5° for A and B, and 1° for C and D. Horizontal scales equal 20 sec for A and B, and 5 sec for C and D.

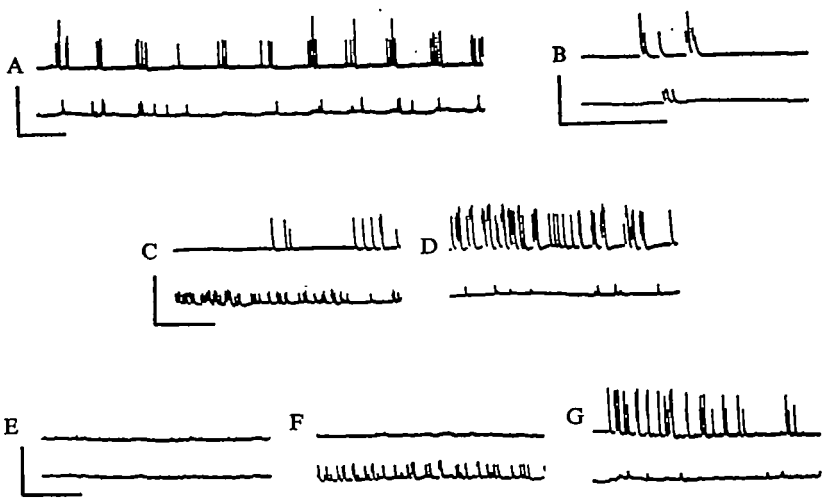

Fig. 3. The ventilatory retractions of the head are mediated by the combined actions of corresponding muscles on the left and right side. The upper and lower traces of each record are intracellular recordings from single muscle fibres of muscles 61 of the right and left side respectively. Rhythmic ventilatory contractions at about 1 Hz are produced by the action of at least two motor neurones to each of the left and right muscles 61 (A and B). In C, the striped drum is moved to the left and this results in decreased output to the right muscle 61 (upper trace) and increased output to the left muscle 61 (lower trace). In D the striped drum is moved to the right with the converse effect. In both cases some ventilatory activity remains. With the connectives between the second and third thoracic ganglia cut, the ventilatory activity completely ceases (E). Activity of the motor neurones can nevertheless still be elicited by movement of the drum to the left (F) or right (G). Vertical scales equal 20 mV throughout. Horizontal scale for A equals 1 sec, and for the remaining records equals 500 msec.

small light source onto the photocells, their output being linearly related to head position. The records of head movement and drum movement, and two channels of intracellular recording were displayed on an oscilloscope (Tektronix 565) and recorded on tape (Thermionic T3000) for later analysis. In the intact insect, various spontaneous non-visually elicited head movements occur such as neck ventilation, head rocking, saccades and tremor (Fig. 2) (Horridge, 1966). To examine optokinetic nystagmus largely in their absence, the second thoracic ganglion was removed unless otherwise stated (Fig. 3) (Thorson, 1966).

The innervation patterns of some muscles were also investigated by graded nerve stimulation combined with the paired intracellular recording techniques described above. The muscle to be investigated was dissected out and pinned down by its cuticle attachments under saline. Motor nerve stimulation or *en passant* recording was usually accomplished using 75 μm silver wire hook electrodes, but suction electrodes were used for the smallest nerves. Several neck muscles are innervated by more than one nerve and so two stimulation channels were provided (Tektronix 161/162). When tension measurement was required, the cuticular attachment at one end of the muscle was held between forceps attached to a mechano-electric transducer (RCA 5734).

RESULTS

I. *Axon types*

Motor axons can be classified in at least two ways and the relationship between these needs some clarification. Axons are often named according to the effect they have on the muscle they innervate – hence a 'fast' axon produces a fast or twitch response, a 'slow' axon produces a slow contraction commencing only above a certain impulse frequency in the nerve, and an 'inhibitory' axon has an inhibitory effect on the contraction produced by the slow (and sometimes the fast) axon.

Alternatively, axons with intermittent or phasic activity are termed 'phasic' axons and those with a steady or tonic activity are termed 'tonic' axons. Activity of a phasic axon is usually associated with rapid contraction of the muscle innervated, whereas activity of a tonic axon is associated with a maintained level of contraction or tonus.

The contraction of a muscle as a whole depends, of course, on the contraction of each individual muscle fibre within the muscle. A single axon may produce quite different responses in different muscle fibres of the same muscle. The former (fast/slow) terminology should therefore only be applied where there is knowledge of both the activity of the axon, and of the *mechanical response of individual muscle fibres.* In practice this is not feasible, and it is usually possible to deduce the fast, slow, or inhibitory nature of an axon from the *electrical* response of the muscle fibres. On the other hand, many axons produce responses that are intermediate between fast and slow or have an activity pattern that falls between phasic (intermittent) and tonic (steady). The latter (phasic/tonic) terminology has the advantage that it can be used without reference to the electrical or mechanical effects of the innervation on single muscle fibres. Since many of the experiments in this work involve a study of normal motor output patterns, the phasic/tonic nomenclature has, in general, been the more useful Thus:

(1) A *tonic* axon is one that has a steady level of activity when the muscle concerned is neither changing its length nor its degree of tension (i.e. when the head is stationary); the axon is also active at increasing or decreasing rates during muscle contraction or relaxation.

(2) A *phaso-tonic* axon is one that is active during contraction or increase in tension of the muscle concerned (i.e. during slow phase of nystagmus), but is inactive when the muscle length is not changing.

(3) A *phasic* axon is one that is active only intermittently or in bursts, this activity occurring during fast contraction of the muscle concerned (i.e. during fast phases of nystagmus); the axon is inactive when the muscle is contracting steadily and also when the muscle length is not changing.

This terminology is correlated with the fast/slow terminology in the following way. A phasic axon usually produces a fast electrically excited membrane response (in phasic fibres) and a fast or twitch response of the muscle (i.e. a phasic fast axon), whereas a tonic axon usually produces PSPs (of various sizes in different fibres) and a slow contraction that depends on the frequency of firing of the axon (i.e. a tonic slow axon). The phaso-tonic axon usually produces a faster response than the tonic slow axon but a slower response than the phasic fast axon and is therefore termed intermediate, but where the phaso-tonic axon to a muscle is the fastest axon present it is termed fast.

II. *Muscle fibre types*

It is even more difficult to obtain a logical terminology for muscle fibre types than for axon types for, whereas axons can be classified by their inherent activity, muscle fibres can be classified in structural terms, in terms of their electrical excitability, or in terms of their responsiveness to the different types of axons innervating them.

Much of the evidence obtained in this work has been in the form of intracellularly recorded responses of single muscle fibres to normal motor neurone activity and it has not generally been possible to correlate the activity of an axon with the *mechanical* response of the muscle fibre it innervates. Individual fibres can, however, be divided into categories with little difficulty on the basis of their large or small PSPs, presence or absence of electrically excited membrane responses, rate of decay of depolarizations and degree of summation of PSPs at high frequency. The extent to which these different responses are due to synaptic differences such as shown in Crustacea by Bittner (1968) as opposed to contractile and excitatory differences, remains to be established.

Where an axon produces a large, fast, electrically excited membrane response in a muscle fibre, that fibre is classified as of *phasic* type (Fig. 4A, E, upper traces).* Only fast axons produce responses of this type and, in phasic muscle fibres, a slow tonic axon produces PSPs that, at low motor output frequencies, may be almost invisible but which increase in size with facilitation (*ca.* 2–5 mV) at higher frequencies. The fast axon responses (*ca.* 15–50 mV) sometimes show slight summation at high frequencies. The time constant of decay of depolarizations in phasic fibres is in the range 4–10 msec. This type of fibre is typical of insect skeletal muscle (see Aidley, 1967; Hoyle, 1957, 1965; Usherwood, 1967). In Crustacea, muscle fibres responding

* It is not possible to be absolutely certain that these large 'spikes' are due to electrically excited responses on top of PSPs rather than merely large PSPs. However, the 'spikes' are considerably larger than other synaptic responses present, and they are shorter in duration which in itself suggests some actuation of the non-synaptic membrane.

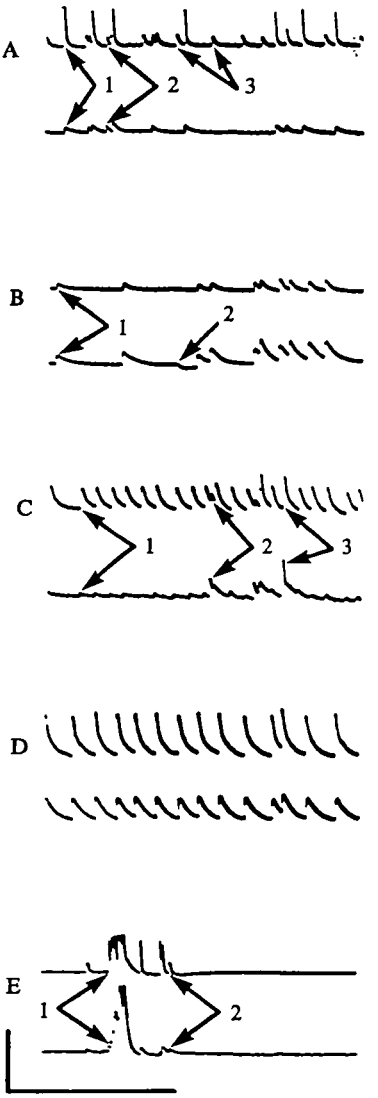

Fig. 4. Intracellular records from pairs of muscle fibres showing the typical responses of different muscle fibre types to normal motor output in the intact insect. (A) Upper trace – phasic muscle fibre innervated by a fast phasic axon (1) that elicits electrically excited membrane responses, and by two slow tonic axons (2 and 3, PSPs). Lower trace – partial synchrony in the two fibres shows that this tonic muscle fibre is innervated by the same fast phasic axon (1) as the fibre of the upper trace and by one of the same slow tonic axons (2), both axons producing only small PSPs. (B) Upper trace – tonic muscle fibre innervated by a slow tonic axon (1, PSPs). Lower trace – super-tonic muscle fibre innervated by the same slow axon (1, PSPs) and also a presumed inhibitory axon (2, IPSPs) that elicits inhibitory postsynaptic potentials (IPSPs) that decrease the size of a succeeding excitatory post-synaptic potential (EPSP). (C) Upper trace – super-tonic muscle fibre innervated by a slow tonic axon (1) and two phasic axons (2 and 3). The two phasic axons produce PSPs that are smaller and larger respectively than those produced by the tonic axon, but have the same long time course. Lower trace – intermediate muscle fibre innervated by the same three axons as the fibre of the upper trace. The two phasic axons produce depolarizations involving varying degrees of electrical excitation, whereas the tonic axon elicits only PSPs. (D) Both the upper and lower traces are from super-tonic fibres both innervated by a tonic axon that produces large PSPs with a long time course, the PSPs showing some summation where they occur close together. (E) Upper trace – a phasic fibre

in the same way to fast and slow innervation (i.e. phasic) have a time constant of 5–10 ms (Atwood, 1963).

Where none of the axons innervating a muscle fibre produce electrically excited membrane depolarizations, that fibre is classified as of *tonic* type. In some tonic fibres the PSPs are small (*ca.* 1–4 mV) (Fig. 4B, upper trace), while in others PSPs as large as 20 mV occur (Fig. 4D, upper trace). The durations of PSPs (*ca.* 19–155 msec) and their time constants of decay (*ca.* 8–40 msec) vary over a wide range and are usually considerably longer than in phasic fibres. However, the distribution of fibres within this range has not been quantified sufficiently to permit dividing the tonic class of fibres into two formally defined subclasses. Nevertheless, to simplify discussion, those fibres showing larger, long-duration PSPs with a long time constant of decay will be referred to as *super-tonic* fibres (e.g. Fig. 4D), while the remainder will be termed *ordinary tonic* fibres (e.g. Fig. 4A, lower trace). Some tonic fibres that at low motor output frequency show small to medium PSPs (1–9 mV) show a high level of membrane depolarization (up to 45 mV) at high motor output frequency due to summation of PSPs (Fig. 4E, lower trace). These fibres, unlike other tonic fibres, are often *not* innervated by a tonic axon, the rapidly summating PSPs being produced by burst activity of a fast phasic motor axon. Fibres responding in this way have not previously been reported in insects, but similar fibres have been found in Crustacea by Atwood, Hoyle & Smyth (1965) who called them *super-sensitive* fibres. This term will also be used here.

A number of fibres do not fall neatly into either the phasic or tonic categories. In fibres classified as *intermediate*, one or more axons may produce membrane depolarizations involving varying degrees of electrical excitability that are not of sufficient magnitude to justify classifying the fibre as phasic (Fig. 4C, lower trace).

Even though there are great differences between some of the fibre types, it is possible that, in reality, each type is but a part of a continuous spectrum. Intermediate fibres probably represent the gradation between phasic and tonic. Similarly, there is probably a continuous gradation between super-tonic and ordinary tonic and perhaps between super-sensitive and ordinary tonic. Nevertheless, the division of the fibres into these categories provides a useful descriptive terminology.

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innervated by a phasic (fast) axon (1) and a phasic (slow) axon (2). The fast axon (1) produces large electrically excited membrane responses, whereas the slow axon (2) produces only small PSPs. Lower trace – a supersensitive fibre innervated by the same axons as the upper fibre. The phasic (fast) axon (1) elicits only slow PSPs at low frequency, but these summate at a high frequency (here *ca.* 200 Hz) to a high level of membrane depolarization, summation continuing with each of up to 10 consecutive impulses at this frequency to reach a depolarization plateau of nearly 30 mV. The second axon (2) elicits only small PSPs. Recording simultaneously from two muscle fibres receiving some common innervation it is usually possible to distinguish those electrical responses that occur as a result of PSPs occasionally exceeding (by facilitation) the threshold for electrical excitation of the fibre, from electrically excited responses produced by a second (fast) axon. Thus, for example, in Fig. 3A, if the activity in the fibre of the upper trace alone were being analysed, all the depolarizations could be attributed to activity of a single axon: all the PSPs are of a similar size and the electrically excited responses could be the result of PSPs exceeding the excitation threshold by facilitation or summation. Similarly, looking at the lower trace alone all the PSPs could be attributed to activity of a single slow tonic axon. Analysis of innervation patterns from paired intracellular recordings greatly reduces the likelihood of making such erroneous conclusions. Vertical scales are as follows: A (30 mV); B, C and D (20 mV); E (40 mV for upper trace, 20 mV for lower trace). Horizontal scale equals 500 msec.

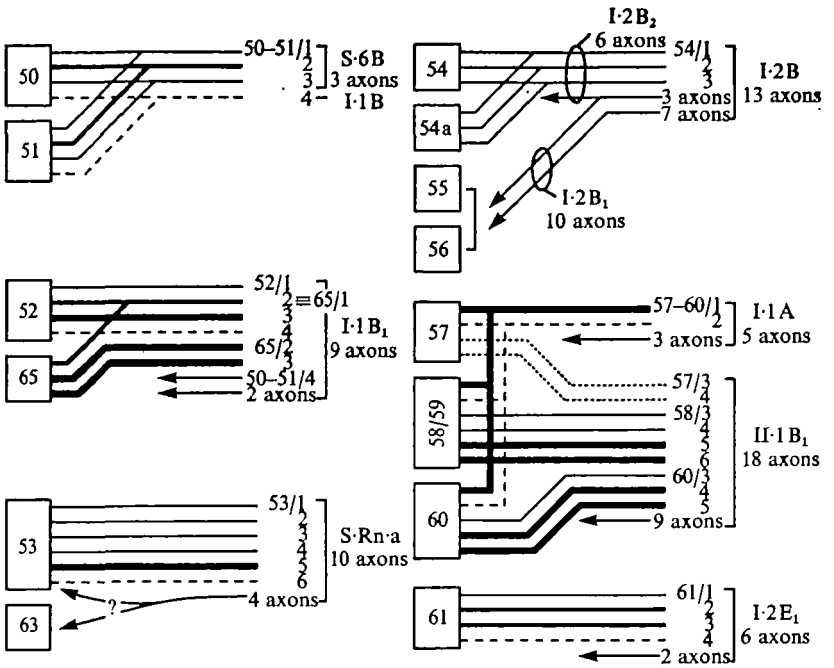

Fig. 5. Origin and distribution of axons to head-moving muscles of the locust neck. Thin lines are tonic (usually slow) axons, medium lines are phaso-tonic (usually intermediate) axons, and thick lines are phasic (usually fast) axons. Dashed lines are probable inhibitory axons. Dotted lines are axons of uncertain type. Arrows indicate the pathways of axons shown histologically but not confirmed physiologically.

III. *Motor output patterns and muscle fibre innervation*

This section comprises the results of intracellular muscle fibre recordings obtained both in the intact animal during visually elicited head movement, and in dissected nerve–muscle preparations in response to nerve stimulation. Results are reported for all the head-moving muscles except muscles 55, 56 and 62. The details included in this section on the motor output patterns to each muscle during optokinetic nystagmus are based on quantitative graphic analyses as shown in Figs. 7 and 8 for muscles 50 and 51. The results for the remaining muscles are summarized in Fig. 12.

(1) *Muscles* 50 *and* 51

The results show that the two muscles receive common innervation from three motor neurones in nerve S·6 (a slow tonic axon 1, a fast phaso-tonic axon 2 and a further slow tonic axon 3) and one probably inhibitory axon (axon 4) in nerve I·1B (Fig. 5) and this conforms with the histological findings (Shepheard, 1973).

The excitatory nature of the three axons in nerve S·6 was shown by graded stimulation of the nerve coupled with intracellular recording from fibres of either muscle, while monitoring tension produced by the muscle pair on their common anterior tendon; stimulation of the nerve with trains of impulses at increasing voltage produces three distinct tension levels.

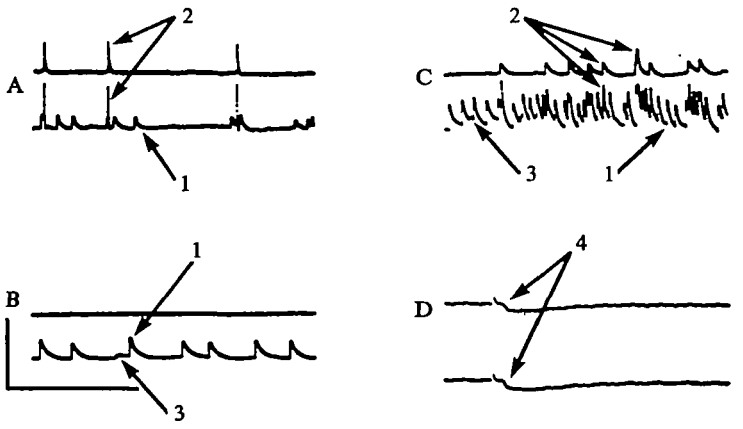

Fig. 6. Intracellular records obtained from muscle fibre pairs in muscle 50 (upper traces) and muscle 51 (lower traces) during visually stimulated head movement in the intact animal (A, B and C) and in response to nerve stimulation (D). In A the slow tonic axon 1 innervates only the fibre of the lower trace where it elicits small PSPs. The fast phaso-tonic axon 2 elicits synchronous electrically excited membrane responses in the two fibres which are correlated with twitch contractions of the muscle pair. These are typical responses of phasic muscle fibres to fast and slow axon innervation. In B and C the fibre of the upper trace is innervated only by the fast axon 2 which produces small PSPs which summate strongly at high frequencies (C). This fibre is therefore classed as super-sensitive. The fibre of the lower traces is innervated by all three excitatory axons, two of which produce large and the third small PSPs, the responses being fairly typical of a super-tonic fibre. The largest PSPs in the lower traces are synchronous with the PSPs in the upper traces which indicates common innervation by axon 2. The next largest PSPs in the lower traces are evidently due to axon 1 while the smallest are produced by output in axon 3. In D hyperpolarizing IPSPs occur in fibres of muscles 50 and 51 in response to stimulation of nerve 1·1B (the motor nerve S·6 to the muscle pair cut).

In the intact insect the neurones have quite distinct characteristics. Their motor output patterns were monitored from intracellular recording from single muscle fibres during visually elicited head movement (see Methods) (Figs. 6–9). When the head is stationary the slow tonic axon 1 is active at a low frequency (5–15 Hz), while the slow tonic axon 3 is barely active. During the slow phases of nystagmus motor output in axon 1 is closely correlated with head movement; during the slow phase in a positive direction† there is a positive trend in the average motor output frequency (Fig. 7, top graph) while during the negative slow phase there is a steadily decreasing trend. These trends in motor output clearly indicate the involvement of the innervated muscles in producing lateral head movement.

Motor output in the fast phaso-tonic axon 2 is also correlated closely with the positive slow phase head movement, the motor output frequency showing a rising trend starting about one-third through the positive slow phase (Fig. 7, centre graph), this activity presumably augmenting the muscular contraction produced by activity of axon 1. The further slow tonic axon 3 shows a negative trend in motor output frequency during the first few seconds of the negative slow phase (Fig. 8, lower graph). Its activity during the positive slow phase was obscured by the larger PSPs of axon 1.

† When intracellular records are taken from a muscle of the right side of the neck, head movement towards the right or ipsilateral side is termed positive while movement towards the left or contralateral side is termed negative. Therefore, when the striped drum moves to the right and electrophysiological records are from the right side, the slow phase of nystagmus will be positive while the fast return phase will be negative.

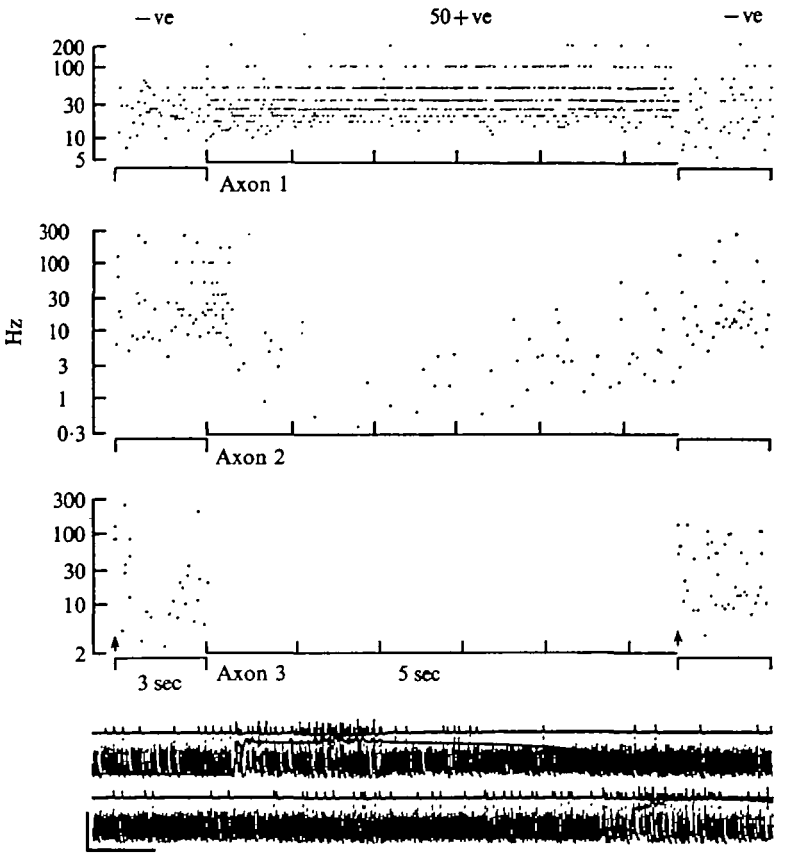

Fig. 7. The motor output in three axons (1, 2 and 3) to muscles 50 and 51 of the right side, recorded intracellularly from a single muscle fibre in each muscle during a positive slow phase of nystagmus to the right, and negative fast phases to the left. The bottom plate shows the intracellularly recorded electrical activity from two different muscle fibres (upper trace from a fibre of muscle 51; lower trace from a fibre of muscle 50), together with attendant head movement. The original record of a complete cycle of nystagmus is here divided into two parts, the first part being placed above the second in the figure. Details of the innervation and fibre types of the two fibres are included in the subscript to Fig. 9 which shows the two fast phases in the above records on an expanded time-scale. The vertical scale below the records represents the calibration for the upper and lower intracellular traces (30 and 20 mV respectively) and for the head movement trace (8°). The horizontal scale equals 2 sec. The instantaneous motor output frequency of each of the three axons to the muscle fibre pair is plotted in the three graphs. The vertical calibration with each graph represents the instantaneous frequency in Hertz. All three graphs are to the same time-scale given beneath the bottom graph. The time-scale of the fast phase is expanded relative to that of the slow phase. The vertical arrows on the time-scale of the bottom graph (axon 3) represent the first impulse after a period of inactivity in that axon.

All three axons are active during the fast phase in either direction. However, the positive fast phase is marked by a high-frequency burst of activity in axons 1 and 2 closely synchronized with the head movement and hence also with a sharp contraction of the muscle pair (Fig. 8). During the negative fast phase, on the other hand, the motor output is switched from a high to a low level, this switching occurring immediately in the case of axon 1 where there is an initial short interruption (or central inhibition) of motor output co-incident with the fast head movement, but rather later

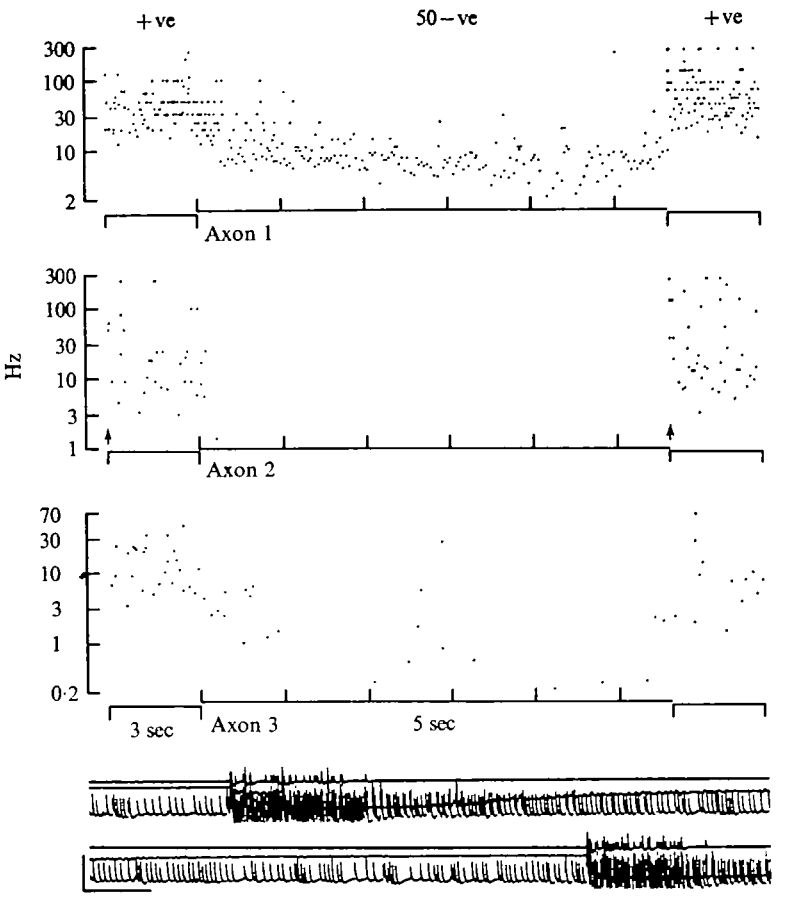

Fig. 8. The motor output in the three axons (1, 2 and 3) to muscles 50 and 51 of the right side, recorded intracellularly from a single muscle fibre in each muscle during a negative slow phase of nystagmus to the left and positive fast phases to the right. Details of the innervation and fibre types of the two muscle fibres are included in the figure subscript of the fast phase expansion (Fig. 9). The vertical scale for the upper and lower intracellular records and head movement trace equals 30 mV, 20 mV and 8° The horizontal scale equals 2 sec.

in axon 2 where extended high-frequency bursts coincident with saccadic head movements persist well into the start of the slow phase (Fig. 7). Since activity of axon 3 was partially obscured, detailed interpretation of its function is not attempted.

Hyperpolarizing PSPs were observed in fibres of both muscles in response to stimulation of nerve S·Rn/I·1 (the presumed inhibitory axon 4 travelling by way of nerve I·1 B_1a), but were never seen in intracellular recordings taken in the intact insect.

Phasic muscle fibres are those most often encountered in muscles 50 and 51 and, together with some intermediate fibres, they comprise the surface layer of fibres in both muscles. These outer fibres are innervated by axon 2 alone, by axons 1 and 2, or occasionally by all three axons. The inner fibres fall into the general class of tonic, some being of the super-sensitive sub-type innervated only by the fast axon 2, others being ordinary tonic or super-tonic fibres innervated either by axons 1 and 2 or by all three axons. Nearly all the fibres in both muscles are innervated by axon 2, about

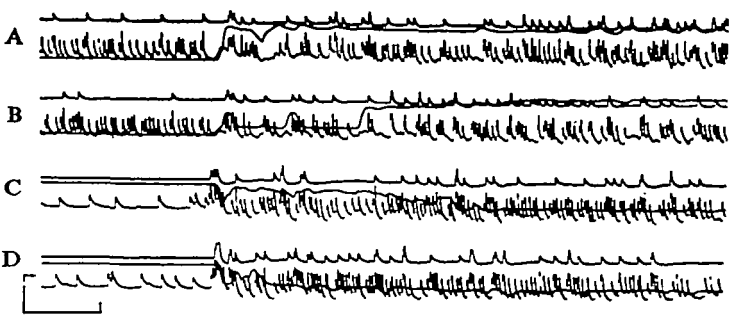

Fig. 9. An expanded time-scale display of the motor output to muscles 50 and 51 of the right side during the first (A) and second (B) fast phase (negative) in Fig. 7, and the first (C) and second (D) fast phase (positive) in Fig. 8. The upper trace in each record is from a super-sensitive fibre of muscle 51 innervated by the fast phaso-tonic axon 2 which elicits small summating PSPs in the fibre. The lower trace in each record is from a super-tonic fibre of muscle 50 innervated by the slow tonic axon 1 which produces large PSPs in the fibre, the fast phaso-tonic axon 2 which produces even larger PSPs which are synchronous with those elicited by the same axon in the first fibre, and a second slow tonic axon 3 which evokes only small PSPs. Vertical scale for the upper and lower intracellular traces and for head movement equals 50 mV, 35 mV and 8°. Horizontal scale equals 500 msec.

half by axon 1, but only a few by axon 3. In the majority of dually or triply innervated fibres the fast axon 2 produces larger depolarizations than the slow axon 1 but in some tonic fibres the reverse is the case. The phasic/tonic distinction between the outer and inner fibres ties in well with the significant differences in size and structure of the two fibre groups (Shepheard, 1969).

(2) *Muscle* 52

The muscle is innervated by nerve $I{\cdot}1B_1$ which contains nine axons (Shepheard, 1973), and which also innervates muscles 50, 51 and 65. Physiologically muscle 52 receives at least four axons (a slow tonic axon 1, an intermediate phaso-tonic axon 2, a fast phasic axon 3, and a possible inhibitory axon 4), one of which (axon 52/2) also innervates muscle 65 (where it is termed 65/1) (Figs. 5, 10).

The muscle contains the full spectrum of muscle fibre types. Most fibres are innervated by two or three of the axons and occasional fibres by all four axons (Fig. 10C, upper trace).

When the head is stationary, the single tonic axon 1 is active at a steady low frequency of about 0·5 Hz. During the positive slow phase two axons are active, the intermediate phaso-tonic axon 2 in addition to the slow tonic axon 1 (Figs. 11A, B, 12). Unlike the situation with muscles 50 and 51, there is no trend in the motor output frequency in either axon during the positive slow phase, although there is a slight negative trend in the motor output in axon 1 for the first few seconds of the negative slow phase. Despite the essential lack of motor output trends, the output is clearly related to the direction of head movement in that axon 1 is active at a somewhat higher maintained frequency during the positive than during the negative slow phase (8 and 3 Hz). This is termed 'setting' of motor output. Axon 2 also shows a setting of motor output in so far as it is active at a steady maintained frequency of about 3 Hz during the positive slow phase, while its activity is completely inhibited during the

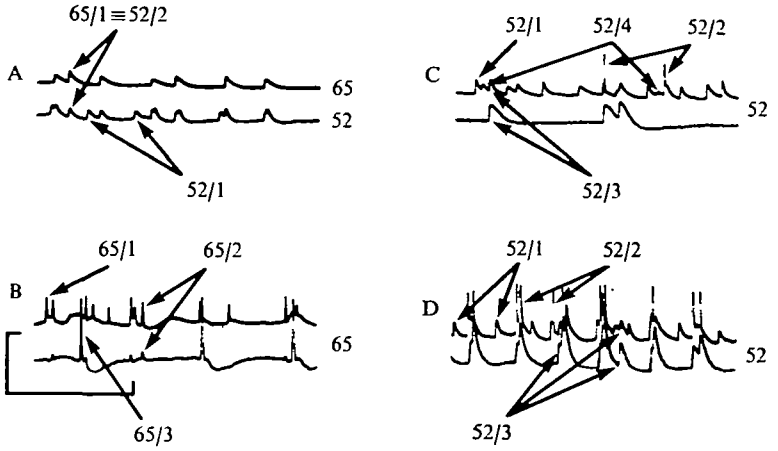

Fig. 10. Intracellular records from muscle fibre pairs in muscles 52 and 65 in the intact animal. (A) Records from an intermediate type of fibre in muscle 65 (upper traces) innervated by an intermediate phaso-tonic axon (65/1 ≡ 52/2), and from a tonic muscle fibre of muscle 52 (lower traces) innervated by the same phaso-tonic axon and also by a slow tonic axon (52/1) during steady contraction of the muscles (positive slow phase). (B) Records from two fibres of muscle 65 during irregular relaxation (first fast phase of Fig. 17G). The upper trace is from an intermediate fibre in the ventral part of the muscle innervated by the phaso-tonic axon (65/1) (medium-sized depolarizations involving a degree of electrical excitation), and by an intermediate phasic axon (65/2) (somewhat larger depolarizations synchronous with small PSPs produced by the same axon in the fibre of the lower trace). The lower trace is from a phasic fibre in the dorsal part of the muscle innervated by the same phasic axon (65/2) (small PSPs), as well as by a fast phasic axon (65/3) (large electrically excited depolarizations). (C, D) Records from a pair of fibres in muscle 52 during negative (C) and positive (D) fast phases. The upper traces are from a phasic fibre of the muscle innervated by the tonic axon (52/1) (medium-sized PSPs), an intermediate phaso-tonic axon (52/2) (large electrically excited depolarizations), a fast phasic axon (52/3) (PSPs or electrically excited depolarizations depending on interspike interval, in each case synchronous with PSPs produced by the same axon in the second fibre), and a slow axon (52/4) (small PSPs). The lower traces are from a super-sensitive fibre innervated only by the fast phasic axon 52/3. This is clearly identifiable as a super-sensitive fibre since the fast phasic axon 52/3 when active at low frequencies elicits only small PSPs (C, lower trace), while at high motor output frequency the PSPs summate to a high level of depolarization (D, lower trace). Vertical scales for the upper and lower traces are as follows: A (50, 20 mV); B (40, 15 mV); C and D (25, 25 mV). Horizontal scale equals 500 msec.

negative slow phase. This differential setting of motor output is presumably correlated with maintained differential tensions, or states of contraction, in muscle 52 during slow phase head movement in opposite directions.

The positive fast phase of nystagmus is correlated with bursts of activity in axons 1–3 (Fig. 12). The motor output bursts in axons 2 and 3 are synchronous during the fast phase (Fig. 10) and this may indicate interaction between the two motor neurones in the CNS or some common interneurone input. The burst activity is closely correlated with irregularities of head movement during the fast phase which indicates that they are directly involved in producing fast contractions of the muscle. Activity in axons 1 and 2 is partially inhibited during the negative fast phase (Fig. 11A). The few spikes in axon 3 during the negative fast phase reflect the fast phase irregularities. Axon 4 is active at its highest frequency just before and during the negative rather than the positive slow phase, and this suggests it might have an inhibitory function even though the PSPs are not hyperpolarizing. Alternatively the axon may be a slow tonic axon.

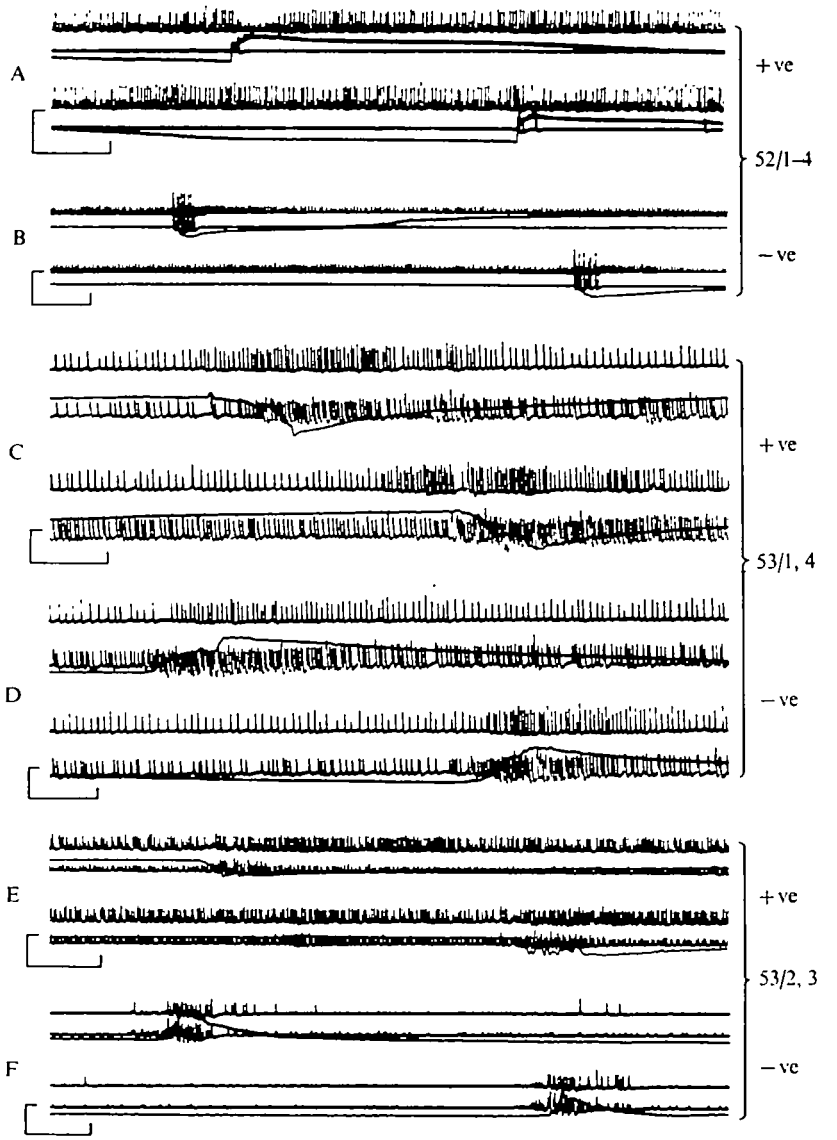

Fig. 11. Motor output to various neck muscles recorded intracellularly from a pair of muscle fibres in each muscle during fast and slow phases of optokinetic nystagmus. (A, B) Innervation as for Fig. 10C, D. (C, D) Two tonic fibres of muscle 53 innervated by the slow tonic axons 53/1 (lower trace) and 53/4 (upper trace). (E, F) Upper traces are from an intermediate fibre of muscle 53 innervated by the intermediate tonic axon 53/2 (large depolarizations) and by the slow tonic axon 53/3 (small PSPs) ('reference' fibre of Fig. 13). Lower traces are from a tonic fibre of the same muscle innervated by 53/3. Vertical scales are as follows: A, B (30 mV, 12°); C, D (15 mV, 7°); E, F (40 mV, 20 mV, 12°). Horizontal scales for A and B equal 5 sec and for C–F equal 2 sec.

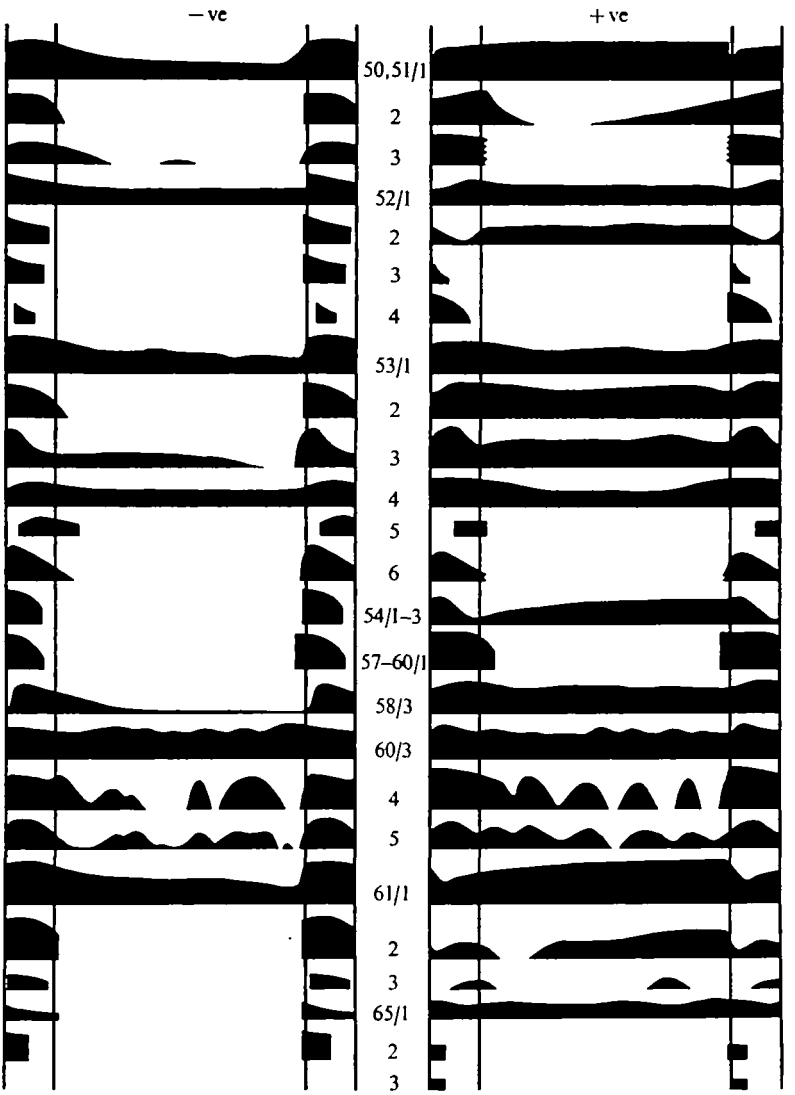

Fig. 12. A combined figure of motor output patterns in each of the identified motor neurones to the neck muscles of one side. In the left column the slow phase of nystagmus is negative (i.e. towards the contralateral side), whereas in the right column the slow phase is positive (i.e. towards the ipsilateral side). The approximate average motor output frequency of each axon is represented vertically on a logarithmic scale where the base-line frequency for each is 1 Hz.

(3) *Muscle* 53

This muscle is unusual in that of the six axons it receives, four are tonic. Three of these are slow axons (axons 1, 3, 4) and one is intermediate (axon 2). In addition, there is a fast phasic axon 5 and a presumed inhibitory axon 6 (Figs. 5, 13).

These six axons may not be the total number innervating the muscle since the nerve S·Rn·a that innervates both muscles 53 and 63 contains 10 axons (Shepheard, 1973).

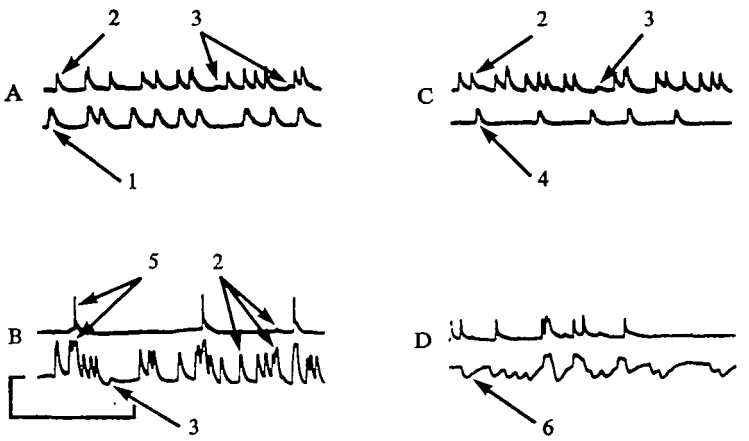

Fig. 13. Intracellular records from various muscle fibre pairs in muscle 53 in the semi-intact insect. In each of the records A–C one of the fibres of the pair is held as a 'reference' fibre, while a second electrode is moved successively to fibres in different regions of the muscle. This reference fibre (upper trace in A and C, lower trace in B) is central in the muscle, is of intermediate type, and is innervated by an intermediate tonic axon 2, a slow tonic axon 3 and a fast phasic axon 5. The second fibre in each of the record pairs is as follows: A (lower trace) – a tonic fibre in the lateral part of the muscle innervated by a slow tonic axon 1; B (upper trace) – a phasic fibre towards the medial side of the muscle innervated by the axon 2 (almost invisible PSPs synchronous with the large PSPs in the reference fibre) and by the fast phasic axon 5; C (lower trace) – a tonic fibre in the medial part of the muscle innervated by the slow tonic axon 4. In D the lower trace is a record from a tonic fibre towards the lateral side of the muscle innervated by an inhibitory axon 6 as well as by one or two tonic axons. The upper trace is from a fibre of similar type and innervation to the reference fibre. A and C are during steady contraction of the muscle (positive slow phases) while B and D are during fast phase head movements. Vertical scales for the upper and lower traces are as follows: A, B and C (40, 20 mV); D (50, 20 mV). Horizontal scale represents 500 msec.

It is probable that some of the four remaining axons provide specific innervation to muscle 63, a muscle which proved too small and inaccessible to investigate.

Although the muscle receives three slow tonic axons, fibres innervated by more than one were only rarely found, the muscle being partially divided by these axons into distinct motor units. The three axons innervate fibres in the lateral (axon 1), centrolateral (axon 3) and medial (axon 4) parts of the muscle respectively. Many fibres in the muscle are multiply innervated by one of the slow tonic axons 1 and 3 in combination with the fast phasic axon 5 and/or the intermediate tonic axon 2. Axon 2 is clearly intermediate between slow and fast, since it produces larger depolarizations than the other tonic axons in commonly innervated fibres, but only small PSPs in phasic fibres of the muscle where the fast phasic axon 5 produces large spikes (Fig. 13). A few fibres are innervated solely by one of the slow tonic axons.

The muscle is divided not only by spatial segregation of the three slow tonic axons but also by virtue of a non-random distribution of muscle fibre types. The lateral fibres innervated by the slow tonic axon 1 are physiologically of tonic and super-tonic type and are distinctively smaller than fibres in other parts of the muscle (Shepheard, 1969). On the other hand, phasic fibres giving electrically excited responses to activity of the fast phasic axon 5 are confined to the medial side of the muscle.

When the head is stationary, the four tonic axons 1–4 are active at frequencies of

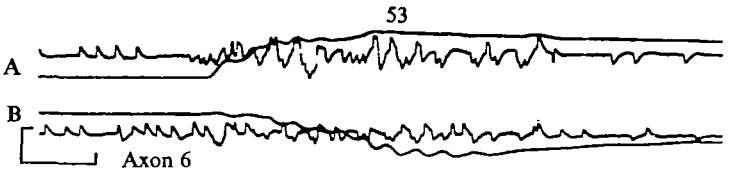

Fig. 14. The motor output to muscle 53 of the left side during a positive fast phase of nystagmus to the left (A), and a negative fast phase to the right (B). The activity is recorded from a tonic muscle fibre innervated by one of the four tonic axons to the muscle which elicits small PSPs, and by the inhibitory axon (axon 6) which elicits small IPSPs (same fibre as in Fig. 13D, lower trace). Fibres innervated by the inhibitory axon are only rarely found and are difficult to 'hold', often showing as here considerable contraction artifact. This suggests fibres innervated by the inhibitory axon are small tonic muscle fibres. The intracellular record is a.c. coupled to increase stability. The axon is active at a high frequency immediately before and during the fast phase in either direction. At these high frequencies (*ca.* 30–60 Hz) the IPSPs summate to increase the polarization of the membrane. Vertical scale for the records equals 20 mV and 5°. Horizontal scale equals 2 sec.

about 12, 3, 4 and 6 Hz respectively. Only two of these axons show any major trends in motor output during the slow phase in either direction, axon 1 has a negative trend during the negative slow phase (Figs. 11D, 12) and axon 3 shows trends directly related to the direction of head movement in either direction (Figs. 11E, F, 12). Axon 3 shows, in addition, a distinct setting of motor output at a higher frequency during the positive than during the negative slow phase, this setting being superimposed on the motor output trends. The motor output in axon 2 is without trend during the slow phases, but the frequency is set at a high level (up to 100 Hz) during the positive slow phase, while it is quite inactive during the negative slow phase. This suggests the muscle is maintained at quite a different tension during lateral head movements in opposite directions.

During the fast phases of nystagmus all four tonic axons show large bursts of activity during both positive and negative fast phases (Figs. 11C-F, 12). A fast axon 5 is phasically active just after the fast phase in either direction (Figs. 12, 15A, B). The impulses occur in pairs and triplets during the positive fast phase which results in a large instantaneous frequency scatter (*ca.* 1–100 Hz). The function of such delayed fast phase activity is not clear, but the activity is clearly correlated with irregularities in the head movement.

Fibres innervated by the inhibitory axon 6 were rarely found. This axon is active at high frequency during and immediately before the fast phase in either direction and at a low frequency during the slow phases (Fig. 14).

(4) *Muscle* 54

The nerve I·2B which contains 13 axons innervates the muscle group 54, 54a, 55 and 56. Six of these axons enter the nerve branch I·2B_2 to muscle 54 and its accessory muscle 54a, and at least the two largest of these enter only this branch to provide specific innervation to this muscle pair (Shepheard, 1973). Methylene-blue preparations show that the three largest of these provide common polyneuronal innervation to many of the fibres, and intracellular records confirm common innervation by two or three tonic and/or phaso-tonic motor neurones (Fig. 5).

All the fibres of the muscle appear to be of similar type (tonic to intermediate) and

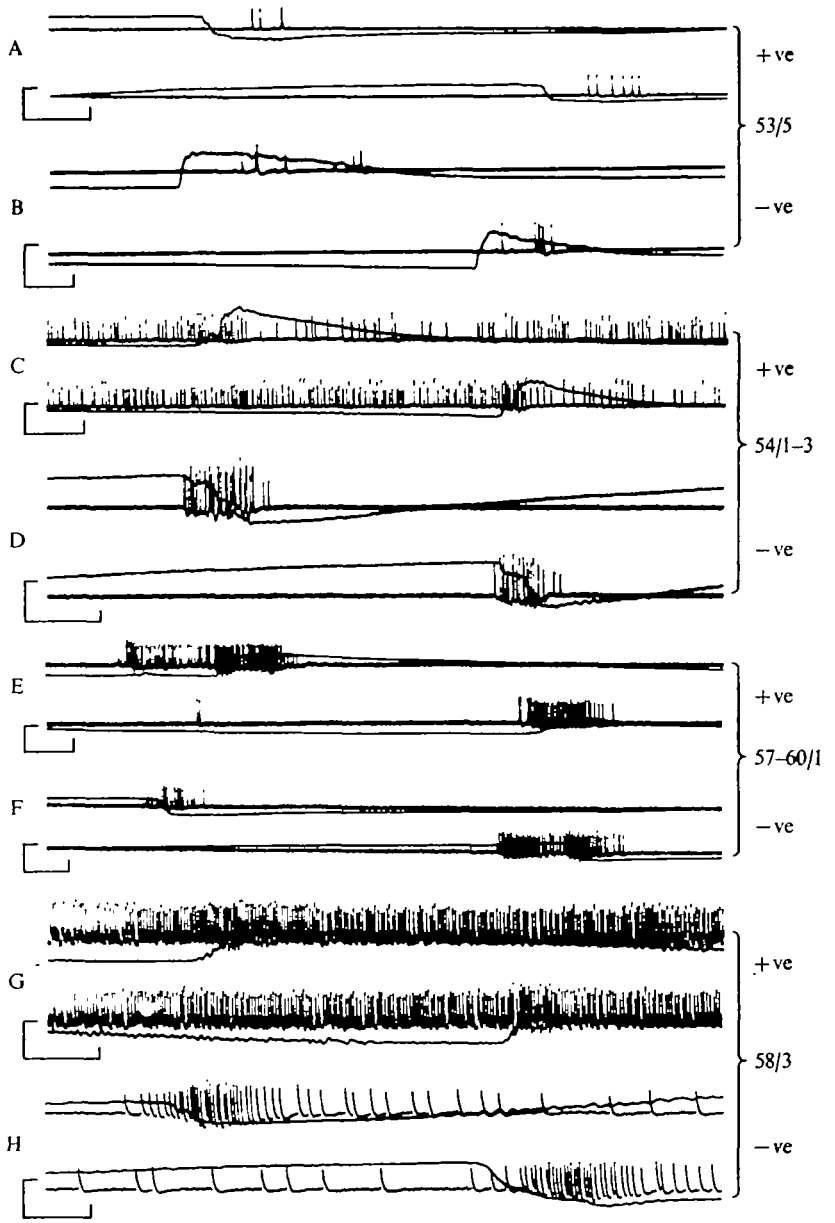

Fig. 15. Motor output to various neck muscles recorded intracellularly from a single muscle fibre in each muscle during fast and slow phases of optokinetic nystagmus. (A, B) Innervation as for Fig. 13 B. (C, D) Records are from an intermediate fibre of muscle 54 innervated by two or three tonic and/or phaso-tonic axons. (E, F) Records are from a phasic fibre of muscle 58 (or 59) innervated by the fast phasic axon 57–60/1. (Innervation by nerve S·Rn/I·1, nerve II·1B_1 cut). (G, H) Records are from a tonic fibre of muscle 58 innervated by the slow tonic axon 58/3. (Innervation by nerve II·1B_1, nerve S·Rn/I·1 cut). Vertical scales are as follows: A, B (40 mV, 5°); C–F (10 mV, 5°); G, H (10 mV, 6°). Horizontal scales equal 2 sec.

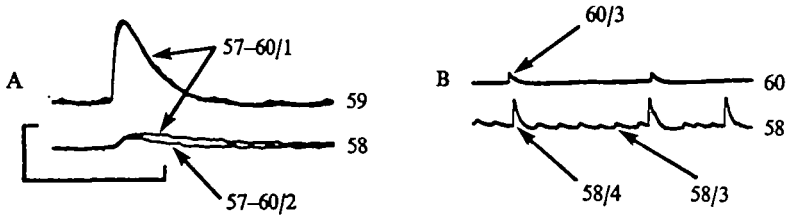

Fig. 16. Intracellular recordings from pairs of muscle fibres in the muscle group 57 to 60. (A) Stimulation of the joint nerve S·Rn/I·1 at two discrete levels superimposed on the one record. Stimulation at the lower level excites the common excitatory neurone 57–60/1 which produces depolarizations in fibres of both muscle 59 (upper trace) and muscle 58 (lower trace). At the higher level of stimulation the PSP in the fibre of muscle 58 (lower trace) is reduced in size and duration, which implies the action of an inhibitory axon (57–60/2). (B) Records from a tonic fibre of muscle 60 innervated by a tonic axon (60/3) (upper trace), and a super-tonic fibre of muscle 58 (or 59) innervated by two tonic axons (58/3 and 4) (lower traces) when the head is stationary, and with nerve S·Rn/I·1 cut through the neck membrane. Vertical scales are as follows: A (10, 10 mV); B (50, 15 mV). Horizontal scale equals 500 msec.

the degree of difference between the depolarizations produced by the different axons was insufficient to enable the activity of the individual axons to be separately determined, and the analysis given (Figs. 12, 15C, D) is therefore of the compound activity of the several axons innervating the muscle.

When the head is stationary the compound motor output frequency is about 4 Hz. During the positive slow phase of nystagmus there is a positive trend in the compound output frequency (2 up to 10 Hz) with a large scatter in instantaneous frequency due to summation of activity of several independent axons. None of the axons is active during the negative slow phase. There is a high-frequency burst of activity correlated closely with the positive fast phase head movement (Fig. 15D) and a somewhat smaller burst associated with the negative fast phase (Fig. 15C). The close correlation of motor output with head movement during both slow and fast phases indicates that muscles 54 are directly involved in producing lateral head movement.

(5) *Muscles* 57, 58, 59 *and* 60

The muscle group receives, on histological evidence, common innervation from at least four of the five axons in the nerve I·1A, and a mixture of specific and partial common innervation from the 18 axons in nerve II·1B_1 (Shepheard, 1973). Two of the axons in nerve I·1A have been confirmed physiologically, one a fast phasic axon (57–60/1) providing common excitatory, and the other axon (57–60/2) providing common inhibitory innervation to each of the muscles in the group (Fig. 5).

The common excitatory motor neurone innervates a large percentage of the fibres of each muscle. In muscle fibres innervated by both excitor and inhibitor neurones, the inhibitory neurone decreases the size of the excitatory PSP (Fig. 16A). Fibres that gave a large response to the excitatory neurone (phasic fibres) are not apparently innervated by the inhibitor (Fig. 16A, upper trace). Fibres innervated by the common inhibitor but not by the common excitor are fairly easily found in muscles 58 and 59. The common excitor is active during the fast phases of nystagmus (Fig. 15E, F), but activity of the common inhibitor was never observed in the intact animal.

Recording in the intact animal (nerve I·1 cut) showed that nerve II·1B_1 supplies

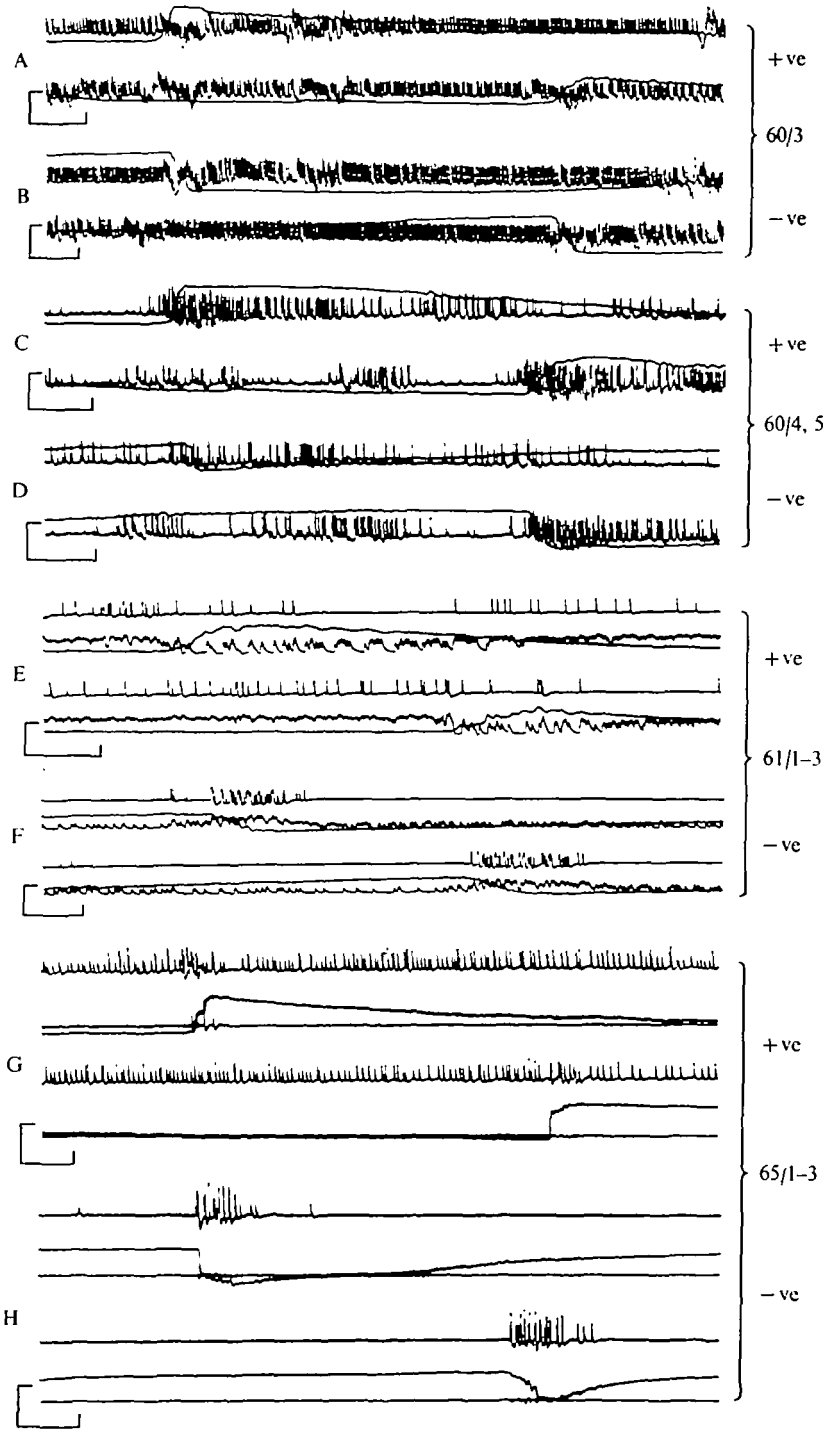

Fig. 17. Motor output to various neck muscles recorded intracellularly from a single fibre of the muscle (A–D) or a pair of fibres (E–H) during fast and slow phases of optokinetic nystagmus. (A, B) Records are from a super-tonic fibre of muscle 60 innervated by the tonic axon 60/3. (Innervation by nerve II·1B_1, nerve S·Rn/I·1 cut). (C, D) Records are from a phasic fibre of muscle 60 innervated by the fast phasic axon 60/4 (large electrically excited depolarizations) and the phasic axon 60/5 (amall PSPs). (Innervation by nerve II·1B_1, nerve S·Rn/I·1 cut). (E, F) Innervation as for Fig. 18 A, B. (G, H) Innervation as for Fig. 10 B. Vertical scales are as follows: A, B (20 mV, 6°); C, D (20 mV, 5°); E, F (80 mV, 40 mV, 8°); G, H (30 mV, 20 mV, 6°). Horizontal scales for A–D, G and H equal 2 sec and for E and F equal 1 sec.

two tonic axons (58/3, 4) and two phasic axons (58/5, 6) to muscle 58 (or 59), and a tonic axon (60/3) and two phasic axons (60/4, 5) to muscle 60. Records from muscles 58 and 59 in the intact animal could not be distinguished since, due to the common point of insertion of the two muscles (Fig. 1), it was not usually possible to be certain of the site of the electrode tip. Dye-marking techniques which could resolve this problem were not used. However, nerve stimulation coupled with paired intracellular recording showed that muscles 58 and 59 receive at least one axon in common from nerve $II{\cdot}1B_1$, while two axons innervate muscle 58 uniquely. In addition, muscle 57 is innervated specifically by two axons from this nerve.

In view of the large number of different axons to several of the muscles in this group (at least 13 to muscle 60), and the small number of fibres in each muscle (*ca.* 20–50) (Shepheard, 1973), it follows that multiple innervation of muscle fibres is to be expected. Such a complex situation is not easy to analyse physiologically, but at least four axons have been shown to innervate some muscle fibres and the majority of single fibres are innervated by one or more axons from each of the nerves $I{\cdot}1A$ and $II{\cdot}1B_1$.

When the head is stationary, the tonic axons 58/3 and 4 and 60/3 are active at average frequencies of about 14, 3 and 2 Hz respectively. Due to the difficulty in obtaining records from the muscle group in the intact insect, the motor output patterns of only a few of the motor axons have been recorded throughout slow and fast phases of nystagmus. During slow phase nystagmus in either direction the two tonic axons 58/3 and 60/3, as well as the fast phasic axons 60/4 and 5 are active (Figs. 12, 15G, H, 17A–D). The tonic axon 58/3 to muscle 58 is the only axon showing any direction-related change in motor output during the slow phase head movements (Fig. 15G, H). The three axons to muscle 60 show neither trends nor setting but show a steadily rising and falling slow phase motor output that is more pronounced in the fast phasic axons 60/4 and 5 than in the slow tonic axon 60/3 (Figs. 12, 17A–D). This cyclical motor output does not occur when the head is stationary but is correlated with lateral head movement, although it is apparently unrelated to the *direction* of that movement. However, the peaks of motor output frequency coincide with the irregularities of head movement that occur at times during each slow phase.

During the fast phases of nystagmus all the axons to the muscle group are active with bursts of activity, the bursts being at particularly high frequency (up to 250 Hz) in the case of the phasic axons 57–60/1, 60/4 and 5 (Figs. 15E, F, 17A–D). Here again the motor output is unrelated to the *direction* of head movement.

The motor output in the common excitor 57–60/1 is interesting in that the fast phase motor output bursts are different in the successive fast phases illustrated (Fig. 15E, F). The first negative fast phase and the second positive fast phase consist of double-peaked bursts where the fast phase head movement coincides with the second frequency peak. Although the muscles 60 apparently receive a normal fast phase motor output in the first burst, their contraction is correlated with only a small head movement, presumably because the other muscles of the neck do not at that time receive a motor output appropriate to the initiation or execution of the fast phase.

Whereas the four muscles 57–60 must act as a single muscle unit in response to activity of the common excitor 57–60/1 during the fast phases, their functions clearly differ in response to control exerted by the motor neurones providing specific innervation to different muscles within the group.

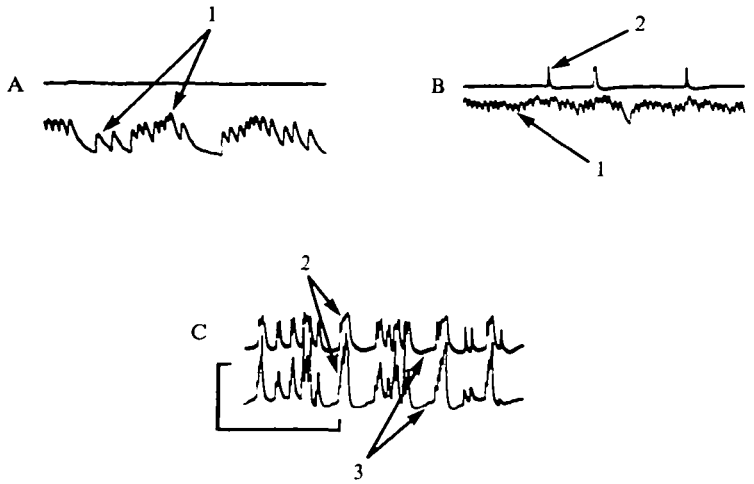

Fig. 18. Intracellular records from muscle fibre pairs of muscle 61 in the semi-intact insect. In A and B the upper traces are from a phasic fibre innervated by a fast phaso-tonic axon 2 (large electrically excited responses), and by a slow phaso-tonic axon 3 (occasional small PSPs not active in the records shown). The lower traces are from a super-tonic fibre innervated by a slow tonic axon 1 (large long-lasting PSPs showing some summation). The phaso-tonic axon 2 may also innervate the latter fibre, but if so it elicits PSPs of the same size and long duration as those produced by the tonic axon. In C the records are from a phasic fibre of muscle 61 (upper trace) innervated by the fast phaso-tonic axon 2 (large electrically excited responses) and the slow phaso-tonic axon 3 (hardly visible PSPs), and from a super-sensitive fibre of the same muscle (lower trace) innervated by the same axons (axon 2 producing strongly summating PSPs, axon 3 producing small single PSPs). The records are during slight contraction of the muscle early in the positive slow phase (A), stronger steady contraction later in the positive slow phase (B), and during jerky contraction in the positive fast phase (C). Vertical scales for the upper and lower traces are as follows: A, B (90, 15 mV); C (75, 20 mV). Horizontal scale equals 500 msec.

(6) *Muscle* 61

This muscle is innervated by nerve $I{\cdot}2E_1$ which contains six axons (Shepheard, 1973). Four of these axons have been confirmed physiologically (a slow tonic axon 1, a fast phaso-tonic axon 2, a slow phaso-tonic axon, 3, and an inhibitory axon 4) (Fig. 5).

The muscle contains the complete range of fibre types encountered. Many ordinary tonic and super-tonic fibres are innervated by the slow tonic axon 1 and not the fast phaso-tonic axon 2, while phasic and super-sensitive fibres are instead innervated by axon 2 but not axon 1 (Fig. 18A, B). Most of the different fibre types seem to be scattered throughout the muscle, but there is one notable exception to this: when the fibres on the anterior dorsal surface of the muscle are penetrated they are usually found to be super-sensitive fibres innervated by axon 2. This axon has a bursty motor output during fast head movements and the small PSPs produced by this fast axon summate to a high level of membrane depolarization at the normal frequency within the burst (*ca.* 150–250 Hz) and these fibres can be seen to twitch in response to these bursts of activity. Fibres of this type are never found in other parts of the muscle. The same axon does, however, innervate phasic muscle fibres in other parts of the muscle and in these fibres it produces an electrically excited response with each nerve impulse (Fig. 18C).

When the head is stationary, the single tonic axon 1 to this muscle is active at widely different frequencies (*ca.* 3–25 Hz) in different preparations. At first sight this

implies innervation by two different tonic axons. However, this is unlikely since, where one fibre of a pair shows slow PSPs to the tonic axon, a similar response in another fibre is always in synchrony.

Axons 1 and 2 both show direction related changes in motor output during the slow phases of nystagmus (Figs. 12, 17E, F). Thus, the tonic axon 1 shows pronounced trends in motor output frequency, positive during the positive slow phase, and negative during the negative slow phase. The phaso-tonic axon 2 shows a positive trend in (average) motor output frequency during the positive slow phase (Fig. 12), with a large scatter in instantaneous frequency due to the presence of spike pairs and triplets in the output. The spike pairs and triplets occur with increasing frequency as the slow phase proceeds and this constitutes a further direction-related trend superimposed on the trend in average motor output frequency. In addition, the output in the phaso-tonic axon 2 shows setting in so far as activity in the axon is completely inhibited during the negative slow phase.

During the positive fast phase of nystagmus axons 1 and 2 both show a burst of activity at high frequency (Fig. 17F), while activity of both is largely inhibited during the negative fast phase (Fig. 17E).

The motor output patterns during both slow and fast phases of nystagmus show clearly that muscles 61 are directly involved in producing lateral head movement. This is entirely to be expected from the anatomical situation of the muscles (Fig. 1).

Activity of the slow phaso-tonic axon 3 is irregular and not related in any clear way to lateral head movement. On the rare occasions when activity of the inhibitory neurone 4 was observed, it was active immediately before and during rapid contractions or relaxations of the muscle in the same way as the inhibitory neurone to muscle 53 (Fig. 14). One of the two remaining axons to the muscle (Fig. 5) may be a fast phasic axon since axons active only during the fast phase were observed on occasion. However, such activity may be due to a less active fast phaso-tonic axon 2 in some specimens.

(7) *Muscle* 65

The muscle receives innervation from at least three axons in nerve $I{\cdot}1B_1$ (an intermediate phaso-tonic axon 1, an intermediate phasic axon 2 and a fast phasic axon 3) (Fig. 5). The nerve $I{\cdot}1B_1$ to this muscle also innervates muscles 50, 51 and 52 and contains nine axons (Shepheard, 1973). One of the axons to muscle 65 (65/1) also innervates muscle 52 (where it is termed 52/2) as has already been described (see *muscle* 52) (Fig. 10). The muscle is unusual in that it receives no tonic innervation – that is, there is no motor output to the muscle when the head is stationary. A related factor may be the small proportion of tonic fibres in the muscle.

During the positive slow phase only the intermediate phaso-tonic axon 65/1 is active (Figs. 12, 17G). This axon shows no trend in motor output frequency but a clear direction related setting of motor-output, the output being zero during the negative slow phase (Fig. 17H).

During the fast phases, the action of axon 1 is augmented by bursts of activity in the intermediate phasic axon 2 correlated especially with the positive fast phase (Figs. 12, 17H). The fast phasic axon 3 is only occasionally active during visually elicited optokinetic nystagmus – in the records shown (Fig. 17G) its activity is closely

correlated with the large irregularities of head movement that occur during one of the negative fast phases. This axon is probably involved mainly in mediating protective retraction of the head, the axon becoming active at quite a high frequency in response to sudden stimuli such as light flashes or puffs of air on the head of the insect. (It should be noted here that the activation was not through the interneurone pathway involved in neck ventilation since that pathway had been interrupted in the usual way by removal of the mesothoracic ganglion).

IV. *Sense organs monitoring head movement*

Little mention has been made so far of variation inherent in the optokinetic response. However, both slow and fast phases of nystagmus can vary considerably in both duration and extent, both between specimens and in the same insect (Fig. 2) and this variation is also evident in the motor output (compare consecutive fast phases in the figures of motor output during optokinetic nystagmus, e.g. Figs. 7, 8, 9, 11 etc.). The variability is presumably in part a reflexion of changing levels of central excitability, but may also indicate the involvement of proprioceptive monitoring of head movement or position.

A number of sense organs may be involved in monitoring head movement. Haskell (1959, 1960) showed that sensory hairs on the cervical sclerites respond to both head movement and position, while a fringe of hairs on the anterior edge of the pronotum responds only to head movement. Goodman (1965) found that when the hair plates of the cervical sclerites are destroyed the locust is unable to hold its body in line with its head, so showing that these proprioceptors were essential for the maintenance of normal head position. Several other sensory structures are present in the neck including a myochordotonal organ consisting of chordotonal sensilla embedded in an elastic strand attached to each of the lateral longitudinal muscles of the neck (muscles 54) (Shepheard, 1973). These proprioceptors are ideally placed to monitor lateral head movement.

The elastic strands of the myochordotonal organs can be easily exposed and cut in the intact animal. With the elastic strand on one side of the neck cut, slow and fast phases of nystagmus are still performed. With the elastic strands of both left and right sides cut, the slow phase becomes slightly irregular but can still be elicited in each direction. The fast phase, however, can no longer be elicited with a continuously moving drum, but can still be produced by rapid drum movements, by light flashes, or by directing a jet of air at the head or thorax. In the intact insect these various stimuli can elicit a fast phase return, provided the head has already traversed through about three-quarters of its normal slow phase extent (Fig. 19).

All the known neck sense organs are innervated by nerve 1·2A (Shepheard, 1973), which can be exposed through the neck membrane just below the ventral cervical sclerite. With one nerve cut, slow phase nystagmus is normal while the fast phase is lost. However, the fast phase can sometimes be elicited as before by any sudden stimulus. With both nerves 1·2A cut, the head often droops slightly, especially when the animal is not stimulated. This drooping is correlated with a generally lower tonic motor output in the unstimulated, de-afferented preparation. Stimulation with a moving striped drum no longer gives fast phases but the slow phases, if a little irregular, can still be elicited in either direction.

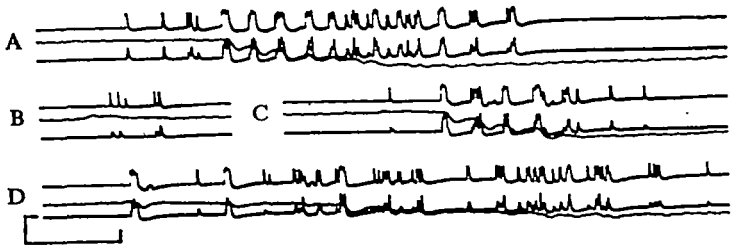

Fig. 19. Intracellularly recorded motor output patterns to muscle 61 and associated head movement, elicited in response to fast drum movements. (A) A normal fast phase elicited by continuous drum movement. (B) A rapid drum movement results in only a small irregularity of head movement. (C) A rapid drum movement elicits a normal fast phase. (D) An irregular fast phase elicited by a rapid drum movement made earlier in the slow phase cycle than was the case in C. Vertical scale equals 80 mV, 40 mV, and 8° for the upper and lower intracellular records and head movement trace respectively. Horizontal scale equals 500 msec.

DISCUSSION

I. *Muscle fibre types and innervation patterns*

In spite of early evidence indicating a range of physiological types of muscle fibre in insects (Cerf, Grundfest, Hoyle & McCann, 1959) it is only recently that many of the physiological and structural bases for such differences have become clear (Cochrane, Elder & Usherwood, 1972). All the neck muscles of the locust contain a range of muscle fibre types distinguished on the basis of their electrical responses to innervation. Only in the case of one muscle (50) have correlations been established between electrical response and structure – the outer fibres of the muscle are phasic and have larger diameter and shorter sarcomeres, whereas the inner fibres of the muscle are tonic and have smaller diameter and larger sarcomeres (Shepheard, 1969). Although simple correlations of this kind have been found before in insects (Hoyle, 1959; Miller, 1969), it is clear from recent work (Anderson *et al.* 1970; Cochrane *et al.* 1969, 1972; Jahromi & Atwood, 1969) that there are many other structural and physiological variables between different types of insect muscle fibre and such correlations have yet to be made in the case of the locust neck muscles.

The response pattern shown here by the super-sensitive fibres has not been previously described in insects. However, the true character of the super-sensitive fibre only becomes apparent at high motor impulse frequency when the PSPs summate to a high level of membrane depolarization; at low frequency the axon elicits only small PSPs typical of a slow axon innervating a tonic muscle fibre, and such fibres could therefore easily have been wrongly identified by other workers. Fibres showing similar, rapidly summating responses and having a non-electrically excitable membrane have been found in certain crustacean muscles (Atwood *et al.* 1965), but the axon eliciting the response is reported as a slow not a fast axon as is the case here. In *Schistocerca*, the fast nature of the axon only became evident when fast, synchronous, electrically excited responses were seen in intracellular recordings taken simultaneously from a phasic fibre of the muscle innervated by the same axon (Figs. 4E, 18C). The results obtained by Atwood *et al.* using single electrode recording techniques may also be interpreted in terms of fast axon innervation.

All but one of the muscles examined receives a slow tonic axon. The single excep-

tion, muscle 65, may not be a true exception since the phaso-tonic axon to this muscle occasionally has a low level of tonic activity. On the other hand, the membrane resting potential of some fibres within this muscle may be above the excitation-contraction (E–C) level resulting in some maintained tension in the absence of excitation as suggested by Usherwood (1967) for other locust muscle fibres.

Several muscles do not receive what is described in this work as a phasic axon, but all but one of these muscles receive instead a phaso-tonic axon with intermediate or fast effect. Only one muscle examined is innervated by more than a single slow tonic axon. However, this muscle, muscle 53, is partially divided into motor units by its three slow tonic axons such that few single fibres are innervated by more than one of these axons. Where the innervation fields of the motor axons are not spatially segregated the axons innervating the muscle are usually of distinct types both as regards their motor output pattern and action. Thus muscle 61 receives a slow tonic axon, fast phaso-tonic, slow phaso-tonic, inhibitory and perhaps a fast phasic axon. Similarly, muscle 52 receives a slow tonic axon, intermediate phaso-tonic, fast phasic and a slow phasic axon.

The largest number of axons previously shown physiologically to innervate a single insect muscle is six (Pearson & Bergman, 1969) and the same number innervate muscle 53. Single muscle fibres innervated by as many as three different axons are commonly found and probably occur in all the neck muscles (e.g. Figs. 4, 6, 13). Four different excitatory axons innervate some fibres of muscle 52 (Fig. 10) and three different excitatory and one inhibitory axon innervate some fibres of muscle 61. This compares with six different axons to some fibres of the posterior coxal levator muscle of the cockroach (Pearson & Bergman, 1969).

II. *Neural control of muscle*

The knowledge gained here on motor output patterns during nystagmus, and innervation and muscle fibre spectrum of different muscles, is sufficient to allow deductions to be made about the function of the different axons to a muscle and the way in which they interact on the different muscle fibre types to elicit various degrees of contraction in, or tension of, the muscle concerned.

The situation will be examined for muscle 61 which is closely involved in *producing* lateral head movement (trends in motor output during nystagmus) (Figs. 12, 17E, F). It contains the complete range of muscle fibre types encountered (phasic, intermediate, tonic, super-tonic and super-sensitive) and it is innervated by at least four physiologically different motor neurones.

The lowest levels of tension are maintained entirely by a low level of motor output in the slow tonic axon 1 (Fig. 12). The tension this axon elicits in the muscle at low frequencies is probably largely due to the response it elicits in the super-tonic fibres of the muscle. Whether or not the axon also elicits contraction in the ordinary tonic fibres will depend on whether the PSPs in that fibre exceed the E–C level for that fibre. It is probable that at low frequencies, the PSPs elicited by the axon in the phasic fibres it innervates are not of sufficient size to exceed the E–C level.

During the first quarter of the positive slow phase, as the output frequency in the tonic axon 1 increases and the muscle begins to shorten, the summating PSPs in the super-tonic fibres (Fig. 17E) are likely to result in progressively increased tension.

The slow PSPs elicited in both the tonic and phasic fibres show facilitation with increased frequency and so both fibre types probably contribute increasingly to the total tension produced by the muscle as the slow phase of nystagmus proceeds.

After the first quarter of the positive slow phase has been negotiated, the fast phaso-tonic axon 2 becomes active with occasional single impulses to augment the action of axon 1 whose activity has by now nearly reached its maximum level. This situation is similar to that in some of the eyecup muscles of the crab *Carcinus* (Burrows & Horridge, 1968). Axon 2 innervates most, if not all, of the phasic, intermediate, and super-sensitive fibres of the muscle, as well as a number of tonic and super-tonic fibres. In the latter fibres it elicits PSPs of similar size and duration to those produced by the tonic axon. These extra PSPs probably have the same effect as a higher frequency of tonic activity, merely adding to the level of depolarization and so increasing the degree of contraction of these fibres. In the phasic fibres of the muscle this axon elicits electrically excited depolarizations which can be seen visually to result in discrete twitches in a number of fibres. At this frequency the axon elicits only small PSPs in the super-sensitive fibres which, however, show small twitch contractions with each impulse. The intermediate fibres usually respond with a small depolarization presumably resulting in a somewhat smaller twitch than that of the phasic fibres.

Pairs and triplets of impulses become increasingly evident in the motor output of axon 2 as the muscle continues to shorten from about one-third of the way through the slow phase (Fig. 17E). In super-sensitive fibres, a triplet of impulses at the high frequency with which they occur (*ca.* 200–250 Hz) elicits a depolarization about three times as large as a single depolarization and, consequently, will result in a much larger contraction of the fibre. The electrical response of intermediate fibres is also frequency dependent. In phasic fibres, however, there is no electrical summation, but the degree of contraction will increase with successive impulses as series elasticity is overcome.

The low level of activity in the slow tonic axon 3 hardly appears to be related to movement of the head during nystagmus (Fig. 12) and what its effect might be on muscle contraction is therefore unclear. The inhibitory neurone is active immediately before and during the fast phase in either direction as in the case of muscle 53 (Fig. 14), and its effect will be mainly on the tonic fibres since inhibitory neurones selectively innervate these rather than phasic fibres. The function of inhibitory axons is discussed more fully in the next section.

III. *Action of inhibitory neurones*

Hyperpolarizing (and presumably therefore inhibitory) postsynaptic potentials have been observed in over half the neck muscles (50, 51, 53, 57, 58, 59, 60 and 61; Fig. 5). In addition, depolarizing postsynaptic potentials may in some cases be inhibitory (Usherwood, 1968) and the axon 52/4 has motor output suggestive of such inhibitory function.

The inhibitory innervation of muscles 50 and 51 is by a single common inhibitor, as also is the inhibitory innervation of the muscle group 57–60. In all cases where recordings of inhibitory activity have been obtained in the intact insect the inhibitory neurones have been active immediately before and during the fast phase in either direction (i.e. during both overall contraction and relaxation of the muscles concerned). This suggests first that common inhibitory innervation is widespread, and secondly

that functionally antagonistic muscles may receive the same common inhibitory innervation. Inhibitory neurones having similar activity patterns have been reported previously in various insects (Hoyle, 1966; Pearson & Bergman, 1969; Pearson & Iles, 1971; Runion & Usherwood, 1968), and some of these are specific inhibitors while others are undoubtedly common inhibitors (Burrows, 1973; Pearson & Bergman, 1969; Pearson & Iles, 1971). Evidence on axon pathways (Shepheard, 1973) shows that as few as two common inhibitors, one in each of the suboesophageal and prothoracic ganglia, could between them innervate all the neck muscles of one side, although the possibility of some of the inhibitors being specific is not ruled out.

Bursts of inhibitory activity immediately before and during the fast phase *relaxation* of a muscle may clearly cause that relaxation. However, it seems strange, at first sight, that the same inhibitory neurone should be active before and during the fast phase *contraction* of the same muscle or of a functionally antagonistic muscle, although such a situation is a necessary concomitant of common innervation. Hoyle (1966) has suggested that in addition to having an inhibitory function, the inhibitory axon to the anterior coxal adductor muscle of *Schistocerca* (termed by Hoyle an 'inhibitory-conditioning axon'), may augment the effect of concurrent excitatory activity in commonly innervated (i.e. tonic) fibres. However, Usherwood (1968) has argued strongly that inhibitory axons can have only an inhibitory effect.

In tonic muscle fibres innervated by excitatory and inhibitory neurones, inhibitory activity probably has little effect in reducing the contraction produced by concurrent excitatory activity (especially where this is fast). However, tonic fibres have a longer relaxation time after excitatory stimulation than phasic fibres (which are not normally innervated by inhibitory axons) and the effect of the inhibitor is to increase relaxation speed (Usherwood, 1968). Thus, common inhibitory activity occurring *before* the fast phase head movement would (rapidly) remove residual tension in all muscles (including functional antagonists) irrespective of their subsequent action. The function of inhibitory activity occurring *during* the fast phases would then be to remove or reduce tension between each of the bursts of motor output, so maintaining each muscle in a state of maximal responsiveness to changing motor output. Such functions are in no way inconsistent with common inhibitory innervation of functionally antagonistic muscles.

IV. *The action of the muscles in concert*

The positive trend in motor output frequency of the tonic and/or phaso-tonic axons to a number of muscles during lateral movement of the head in one direction, and the negative trend in the motor output frequency during movement of the head in the reverse direction, suggest these muscles are directly involved in *producing* lateral head movement. These are muscles 50, 51, 54 and 61 (Fig. 12). The motor output to several other muscles is, however, set and maintained at quite a different level during the slow phase in opposite directions, which suggests such muscles are involved rather differently in controlling head movement. Two pairs of muscles showing particularly pronounced setting are muscles 52 and 65 (Fig. 12).

In some cases, one axon to a muscle may demonstrate a striking setting effect while other axons show trends in their motor output frequencies during the slow phase of nystagmus. For example, of the axons to muscle 53, one (axon 4) shows neither trends

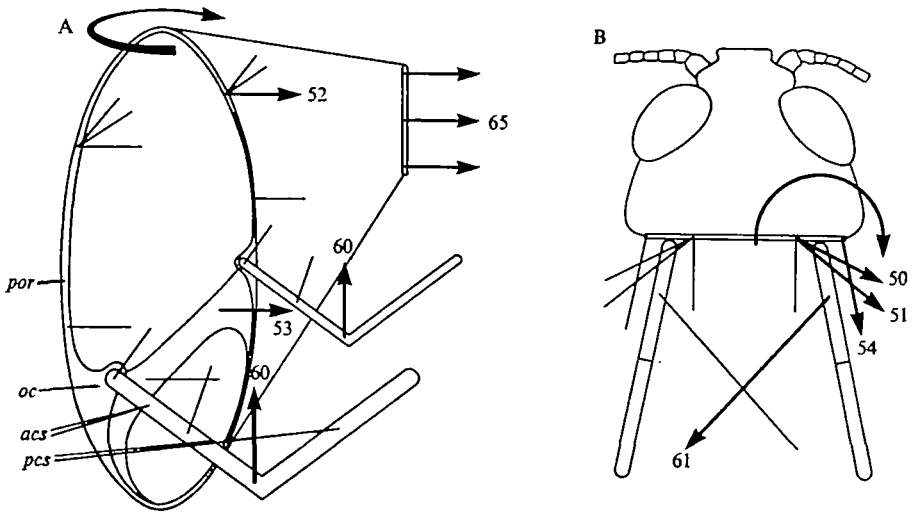

Fig. 20. The action of some of the neck muscles during head movement to the right, showing the way the muscles rotate the head on a fulcrum formed by the 'ball and socket' joint at the junction of the anterior cervical sclerite of the right side with the post occipital ridge of the head. The fulcrum is maintained by one set of muscles (52, 53 and 65 – arrows in A), while head rotation is produced by the simple contraction of a second set of muscles (50, 51, 54 and 61 – arrows in B). *acs*, anterior lateral cervical sclerite; *pcs*, posterior lateral cervical sclerite; *por*, postoccipital ridge. Not to scale.

nor setting, another (axon 1) shows merely a slight trend, another (axon 3) shows slight trends and slight setting while a further axon (2) shows very pronounced setting and no trends. The significance of the setting effect becomes clear when one considers the anatomical placing of those muscles that show the effect.

The head is only loosely suspended on the prothorax, the only 'joint' being provided by the lateral cervical sclerites embedded in the neck membrane. The anterior and posterior lateral cervical sclerites are hinged to allow the anterior sclerite to fold back on the posterior, and each anterior sclerite is fixed (through the occipital sclerite) to a 'ball and socket joint' (the occipital condyle) at the side of the head (Figs. 1, 20). These sclerites provide support for each side of the head while also allowing considerable freedom of movement in the vertical, horizontal and roll planes. Probably the most important function of the sclerites is to mediate extension of each side of the head. Were it not for their existence, head extension could not be produced directly by muscular contraction.

Several muscles originating dorsally on the prothorax provide direct support to the sclerites. Muscles 58 and 59 act on the occipital sclerite and anterior lateral sclerite respectively, while muscle 60 effectively acts at the joint between the anterior and posterior lateral sclerites. Thus while all three together provide a lifting action, muscles 57 and 58 would tend to fold the anterior sclerite on the posterior sclerite and muscle 60 would tend to extend the sclerites. The action of these muscles alone would prevent the head as a whole from dropping but, since the sclerites are attached to the head at one point only (through the occipital condyle), the action of these muscles would not prevent the head from tipping forwards.

A single backwards tension applied to the top of the head would be sufficient to hold the head in an upright position. Several muscles in combination serve this function – the dorsal longitudinal muscles 52, the dorsal neck muscles 65 and the two pairs of muscles 55 and 56. The motor output to muscles 55 and 56 was not investigated, but muscles 52 and 65 are the same muscles in which the setting tendency is most pronounced. The effect of setting of the motor output frequency on the supportive action of the muscles will first be considered as regards the pair of dorsal longitudinal muscles 52 in isolation. When the head is stationary, the single tonic axon 1 to the left muscle and the corresponding axon to the right muscle have a similar level of activity. When the drum commences to move, say to the right, the motor output frequency in the tonic motor axon to the right muscle rises and that in the axon to the left muscle falls. In addition, the phaso-tonic axon 2 to the right muscle becomes active. Whether the head is stationary, moving to the left or moving to the right, the supportive action of the muscles must remain constant if the head is to remain at the same level. The explanation of setting would therefore seem to be that when the head is stationary both the left and right muscles contribute equally to the support of the head, but that as soon as the drum starts to move to the right, the tension in the right muscle rises and that in the left muscle falls with no length changes of either muscle, while the joint backward tension of the muscle pair on the head remains constant. The head is then no longer prevented from falling forward by the *two* muscles, each applying a backward force at a different point on the head, but by *one* muscle applying the same total force at only a single point on the right side of the head. The setting of the motor output to all the other muscles can be looked upon either as a part of, or as a compensation for, the shift in weight of the head to an off-centre position at the commencement of head movement.

With the commencement of drum movement to the right, the tonic axon 1 to muscle 52 of the right side, the phaso-tonic axon 52/2 to muscles 52 and 65 of the right side and the tonic axon 2 to muscle 53 of the right side all show a rapid increase in their motor output frequency to a set level which is maintained without change throughout the slow phase to the right (Fig. 12). As a result of this setting effect, the tension in each of these muscles is increased, while that in the same muscles of the other side is decreased. The increased tension in the ventral longitudinal muscle 53 will offset the increased backward force on the upper right side of the head produced by the increased tension in muscles 52 and 65 and stability of the system is thus preserved.

The relationship to the occipital condyle of the insertions of each of the muscles 52, 53 and 65, is most significant (Fig. 20). Muscle 52 of the right side exerts its backward force immediately on to the upper right side of the head above and to the right of the occipital condyle. The backward force of muscle 65 of the right side is distributed through the neck membrane over a large area of the dorsal right side of the head to the upper right of the occipital condyle. Muscle 53 of the right side exerts its backwards force on the head at a point situated to the lower left side of the right occipital condyle. The three muscles thus exert their backward force in a triangular arrangement around the occipital condyle of that side. These three muscles between them have therefore established a single fulcrum for rotation of the head – the occipital condyle of one side – while at the same time maintaining the same supportive action to the

head previously provided by these muscles together with their contralateral opposite numbers. Once the fulcrum has been established as the occipital condyle of the right side by the setting of the motor output to the appropriate muscles, the slow phase towards that side is then *produced* mainly by the action of muscles 50, 51, 54 and 61 – those muscles which receive a motor output showing a strong trend during the slow phase.

The tension changes that occur with setting during slow phase head movement to the right result in an increased backward force on the fulcrum of that side. This force acts to fold the ventral sclerites of the right side, and is offset, and the folding controlled, by the rising and falling output to muscle 60 (Fig. 12) so allowing the folding to take place in a series of discrete steps. Similarly, the sclerites of the left side are extended in stepwise manner by the action of muscle 60 of the left side. Thus while the head is rotated to the right (on the fulcrum provided by the right occipital condyle), the fulcrum of the right side is retracted and that of the left side extended so adding a further rotational component of the head in the same direction.

In spite of the anatomical complexity of the neck musculature and innervations, a single stable fulcrum for lateral head rotation is thus established by output in a very few motor axons, and the head is rotated on this fulcrum by the simple direct action of only a few muscles.

V. *Central versus peripheral control*

The results show that a complex slow phase motor output programme is built into the central nervous system, and that the programme is set in motion in response to, and at a rate depending on, the relative movement of the visual field and that this programme can be elicited entirely in the absence of proprioceptive feedback.

The loss of the fast phase in the de-afferented preparation suggests, however, that completion of the slow phase must be signalled back to the central nervous system before the fast phase motor output programme is elicited. This is unlike the situation in the crab *Carcinus* (Burrows & Horridge, 1968) where both the fast and slow phase motor output patterns can be elicited by a moving striped drum in the absence of proprioceptive feedback.

A role for the proprioceptors during the slow phase of nystagmus may be indicated by the slightly increased irregularity of the slow phase in the de-afferented preparation. In the intact insect the proprioceptive feedback may enable the central nervous system to modify small inherent errors in the visually driven motor output programme so enabling fine co-ordination of the response. In addition, the decline in tonic motor output in the stationary head in the absence of feedback implies a generalized central nervous excitatory function.

SUMMARY

1. Head movement in the locust *Schistocerca gregaria* is mediated by 14 pairs of muscles. The normal motor output to many of these muscles has been investigated in the intact insect by recording with two intracellular microelectrodes from different fibres of a muscle during slow and fast phases of optokinetic nystagmus elicited by rotation of a striped drum in the visual field. In addition, details of the innervation pattern and muscle fibre spectrum of the muscles have been investigated

by paired intracellular recording during graded stimulation of the motor nerves in the dissected preparation. Of more than 60 different axons shown histologically to innervate the neck muscles on each side, the activity of about 25 have been analysed and deductions are made about the way the muscles work together in concert to produce head movement.

2. At least four physiologically distinct types of axon innervate several muscles. These types are tonic (slow), phaso-tonic (intermediate), phasic (fast) and inhibitory. Stationary head positions are maintained by low levels of motor output in the tonic axons alone, these axons also being mainly responsible, when active at higher frequency, for producing small slow head movements. Phaso-tonic axons become progressively more active during larger or faster head movements to augment the effect of tonic axon activity. The fastest head movements are correlated especially with activity of the phasic axons. Inhibitory neurones are active during and immediately before rapid head movements, the output to individual muscles being correlated with both contraction and relaxation.

3. On the basis of their electrical responsiveness to the axons innervating them, muscle fibres have been classified into the following types: 'phasic', 'intermediate' and 'tonic', with the tonic class subdivided into 'ordinary tonic', 'super-tonic' and 'super-sensitive'. Some muscles contain only a small range of fibre types, while others contain the complete range. Deductions are made about the way the different axon types interact on the different muscle fibre types to elicit various degrees of contraction or tension.

4. The slow phase motor output patterns are the result of a centrally determined programme elicited by visual input (rotation of the striped drum), and are not dependent on, but may perhaps be modified by, proprioceptive feedback. On the other hand, the fast phase of nystagmus is initiated by the central nervous system only after reference to the proprioceptive input from various sense organs of the neck and prothorax.

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