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# PHYSIOLOGICAL IDENTIFICATION AND ASYMMETRY OF LOBSTER CLAW CLOSER MOTONEURONES

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SUMMARY

The somata of the fast closer exciter (FCE) and slow closer exciter (SCE) motoneurones to the dimorphic claw muscles of the lobster *Homarus americanus* were physiologically identified in an isolated claw-ganglion preparation, by recording from a cell body simultaneously with recording from an identified axon. The FCE, SCE, and opener exciter (OE) somata are the largest cells in the anterior ventral region of the ganglion and appear consistently as a triad. A marked asymmetry occurred in the responsiveness of the identified FCE and SCE somata to sensory stimulation via the 2nd root. The SCE soma produced a longer burst with higher spike frequencies than the FCE soma in either cutter or crusher claw. When homologous somata were compared, the crusher FCE and SCE produced higher frequencies and longer bursts of spikes than their cutter counterparts. Since this occurred in response to both sensory stimulation via the 2nd root and depolarization of the soma it suggests that differences in motor output between homologous motoneurones have an extrinsic and intrinsic origin. Furthermore, asymmetry sometimes occurred within an individual motoneurone with a larger number of spikes in the soma than in the axon. Thus the homologous FCE and SCE motoneurones are differentiated into physiologically different types.

## INTRODUCTION

Since the beginning of the century there has been considerable interest in explaining how the paired chelipeds (claws) of certain crustaceans, which show bilateral asymmetry of the other appendages, become dimorphic (Wilson, 1903; Przibram, 1931; Darby, 1934). In this condition, one of the paired chelipeds is the major claw (crusher or snapper) and the other the minor claw (cutter, ripper or pincer), both differing in size and external morphology. The paired closer muscles of the claws also reflect this dimorphism in two species that have been examined intensively, namely lobster *Homarus americanus* and shrimp *Alpheus*. In both species the closer muscles are asymmetric in terms of their contractile responses (Wiersma, 1955; Govind & Lang, 1974; Ritzmann, 1974), fibre composition (Jahromi & Atwood, 1971; Lang, Costello & Govind, 1977; Costello & Lang, 1979; Stephens & Mellon, 1979) and motor patterns

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(Govind & Lang, 1974; Stephens & Mellon, 1979; Mellon & Stephens, 1979; Costello, Hill & Lang, 1980).

Recently interest in understanding how dimorphism occurs has been rekindled by the discovery that claw and closer muscle asymmetry may be experimentally altered in lobsters and shrimps. By rearing early juvenile (4th and 5th stage) *Homarus* in substrate-free containers, differentiation of the crusher claw is inhibited and the animals have paired symmetrical cutter claws (Lang, Govind & Costello, 1978). This experiment suggests a possible causal relationship between use and disuse of the claws and their differentiation into cutter and crusher types. In *Alpheus* the asymmetry may be altered in adults whereby sectioning of the snapper cheliped nerves causes transformation of the opposite pincer claw to a snapper claw (Mellon & Stephens, 1978). This experiment unequivocally demonstrates the influence of the nerve in determining claw and closer muscle differentiation, though it does not distinguish between sensory and motor nerves. However, Lang *et al.* (1980), by correlating muscle fibre histochemical properties with innervation patterns in the claw closer muscles of lobster, argue that it is the motoneurones which exert trophic influences on muscle fibre differentiation. Certainly there is good evidence that the motoneurones of vertebrates have a profound influence upon the differentiation of fast and slow muscle (Guth, 1968; Gutmann, 1976).

In this paper we have examined the physiological responses of identified motoneurones in the closer muscles of the dimorphic claws of *Homarus*, and have found differences between motoneurones in claws of one type and their homologues in the other.

## MATERIAL AND METHODS

Adult lobsters *Homarus americanus* weighing approximately 500 g were used throughout the study. They were bought commercially or caught in local waters and maintained at ambient temperatures (*ca.* 20 °C) in running sea water at the Marine Biological Laboratory, Woods Hole. They were fed live mussels or fish three times per week. The isolated claw-ganglion preparation used in this study was adapted from that described by Wiens (1976) for the crayfish. A lobster with vigorous reflexes was bled by removing all its walking legs at the base. Next it was placed ventral side uppermost in a Y-shaped Perspex chamber designed to hold the body in the median trough and the paired claws in the two lateral troughs. The lobster was immobilized in this position with dental wax and immersed in a physiological medium of the following millimolar composition: NaCl, 472; KCl, 10; $CaCl_2$, 16; $MgCl_2$, 7; Tris HCl, 10; maleic acid, 10; and glucose, 11. The bathing fluid was oxygenated throughout the experiment. A cooling coil in the chamber gradually lowered the temperature of the bathing fluid from approximately 20 °C (room temperature) to 10–12 °C over a period of 1–2 h. During this time the closer nerve, overlying the stretcher muscle, was exposed in the carpus and part of the closer muscle in the propus (Fig. 1A).

Next the 1st thoracic ganglion together with the 1st and 2nd roots were exposed by removing the overlying exoskeleton with fine bone rongeurs. Usually the dissection extended anteriorly to the suboesophageal ganglion and posteriorly to the 2nd thoracic ganglion. The longitudinal connectives were cut anteriorly at the base of the sub-

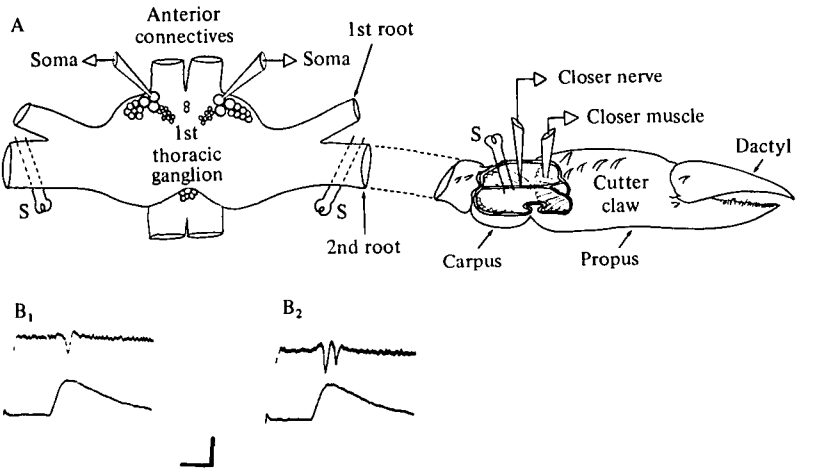


Fig. 1. (A) Isolated claw-ganglion preparation in lobster, *Homarus americanus*, showing placement of stimulating electrodes (S) on 2nd root of ganglion and on closer nerve in the carpus. An extracellular electrode is placed on the closer nerve to monitor spike activity, while intracellular electrodes monitor activity in a closer muscle fibre and in the somata. (B) Stimulation of the closer nerve elicits an orthodromic axon spike and antidromic soma spike (B 1) both belonging to SCE, because the FCE axon spike (B 2) which has a faster conduction velocity is activated at a higher threshold. Vertical calibration: 4 mV. Horizontal calibration: 10 ms.

oesophageal ganglion and posteriorly at the apex of the 2nd thoracic ganglion. The ganglion was freed completely by cutting all the connective tissue strands attaching on its surface. By cutting the base of the claws from the thorax, the body of the lobster could be removed, leaving the 1st thoracic ganglion suspended between the paired claws by its 1st and 2nd roots.

The ganglion was pinned by its connectives to a Sylgard-covered Perspex platform placed underneath it. The platform housed a mirror, and the ganglion could now be viewed with indirect light. The ventral surface of the ganglion was desheathed with iridectomy scissors and the spongy connective tissue removed by gentle jets of water current. This exposed the somata located in a large cluster in the anterior ventral edge (Fig. 1 A). The fully dissected isolated claw-ganglion preparation is shown in Fig. 1 A with the usual arrangement of stimulating and recording electrodes. In the carpus a pair of platinum wires were used to stimulate the closer nerve with brief (0·1 ms) electrical pulses. The resulting action potentials in the closer nerve were monitored more distally by a suction electrode and the excitatory junctional potentials (EJPs) in the closer muscle fibre by an intracellular electrode. Recordings at the periphery served to identify the FCE and SCE axons, which could then be stimulated selectively in order to idenfity their respective somata. Recordings were made from individual somatas using glass microelectrodes (20–40 MΩ). In order to provide a source of sensory stimulation which would be fairly standard, the 2nd root was stimulated with long (0·2 ms) pulses via paired platinum wire electrodes.

The amplification, display and recording of the physiological data was by conventional methods.

## RESULTS

### *Physiological identification of FCE and SCE somata*

The FCE axon to the claw closer muscle has a higher conduction velocity than the SCE axon (Govind & Lang, 1974) and the axons (at the periphery) may be reliably differentiated on this basis (Fig. 1 B). Also the FCE axon usually has a higher threshold for stimulation than the SCE axon (Fig. 1 B) and this allows for selective stimulation of each axon in order to locate their somata in the 1st thoracic ganglion. Therefore, in the isolated claw-ganglion preparation (Fig. 1 A), the FCE and SCE axons are identified in the propus by the above methods and sometimes also by the contraction they evoke. The FCE causes a twitch with a single or twin pulse whereas the SCE causes tonic contraction with several pulses (Wiersma, 1955; Govind & Lang, 1974).

Fig. 2 demonstrates the various physiological tests used to idenfity a particular soma as belonging to the SCE axon. Thus, in one preparation (Fig. 2A), stimulation of the SCE axon in the closer nerve in the carpus elicited an orthodromic SCE axon spike and an antidromic soma spike. The soma spike had a latency of 15 ms and the distance between the stimulating electrode in the carpus and the soma in the ganglion was approximately 100 mm. Since the conduction velocity of the SCE axon is 8·4 ms (Lang & Govind, 1977), the delay of 15 ms is sufficient for the impulse to travel back to the ganglion and invade the soma. In this same preparation the FCE axon had a higher stimulus threshold and its spike is seen at a higher stimulus voltage (Fig. 2 B) as preceding the SCE axon spike. The axon spikes were also correlated with muscle EJPs (Fig. 2 C) in the area of the closer muscle known to be innervated only by the SCE axon. In another preparation, spikes in the soma were matched 1:1 to axon spikes in the closer nerve (Fig. 2 D) previously identified as SCE axon spikes by the slow contraction they elicited. In this same preparation the spontaneous burst of axon spikes were inhibited when hyperpolarizing current was injected into the soma (Fig. 2 E) and accelerated when the soma was depolarized (Fig. 2 F).

The physiological criteria for identifying the FCE soma are given in Fig. 3. Sensory stimulation (via the 2nd root) with increasing intensity gave initially only an exictatory postsynaptic potential (EPSP) in the soma (Fig. 3 A), followed by an EPSP which developed into a spike in the soma (Fig. 3 B). Corresponding with the soma spike was an axon spike in the closer nerve and a muscle EJP in an area known to be innervated by the FCE axon only (Fig. 3 B). A further increment in stimulating voltage resulted in two soma spikes matched to two axon spikes and muscle EJPs (Fig. 3 C). In a second preparation, stimulation of the FCE axon in the closer nerve, with single (Fig. 3 D) or twin (Fig. 3 E) shocks, gave an orthodromic axon spike or spikes and soma spikes. The response in the soma appeared after a delay of 13 ms. Since the conduction velocity of FCE axon is 9·6 ms (Lang & Govind, 1977) and the distance between the stimulating electrode and the soma was approximately 110 mm, the latency of 13 ms was adequate time for the impulse to invade the soma. Finally, when this soma was depolarized, a spike which resembled the FCE axon spike was recorded in the closer nerve (Fig. 3 F).

The location of the FCE and SCE somata is shown in Fig. 4 together with the soma of the exciter neurone to the claw opener muscle. The opener exciter (OE) soma was

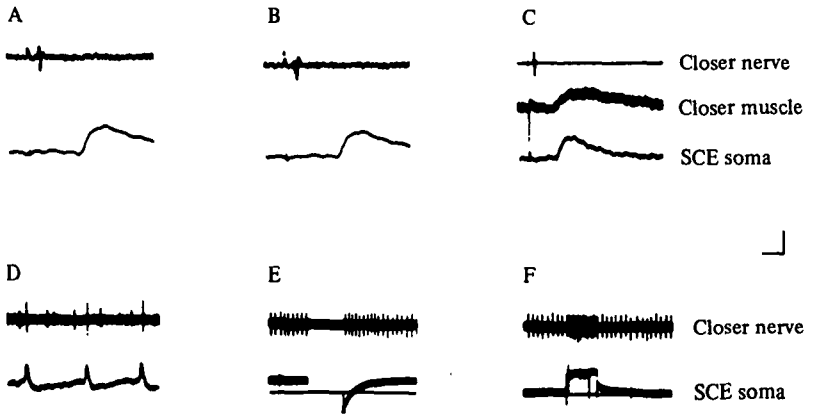


Fig. 2. Physiological identification of SCE soma by following criteria. (A, B, C) Recording antidromic soma spike and orthodromic axon spike and muscle EJP in response to stimulation of SCE axon. (D) Correlating axon and soma spikes during spontaneous activity. (E, F) Hyperpolarizing and depolarizing soma to inhibit and accelerate spontaneous axon spike activity respectively. Vertical calibration: 4 mV in (A, B, C, D). Horizontal calibration: 10 ms in (A, B); 20 ms in (C); 0·2 s in (D); 4 s in (E, F).

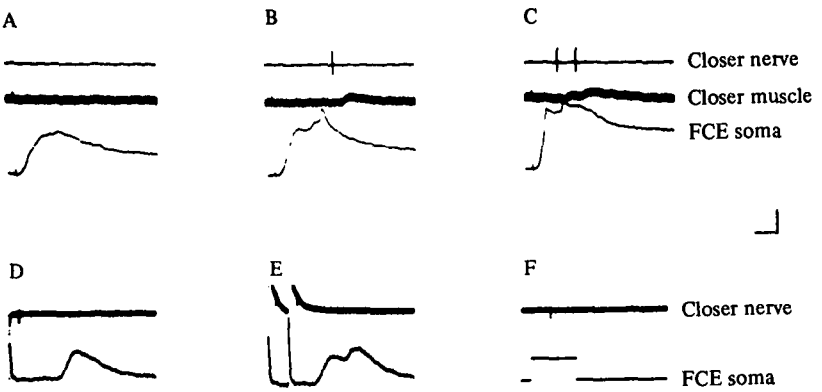


Fig. 3. Physiological identification of FCE soma by following criteria. (A, B, C) Correlating soma spike, muscle EJP and axon spike with 2nd root stimulation. (D, E) Recording antidromic soma spike and orthodromic axon spike when FCE axon stimulated. (F) Eliciting FCE axon spike with depolarization of soma. Vertical calibration: 4 mV in (A, B, C); 2 mV in (D, E). Horizontal calibration: 40 ms in (A, B, C, F); 10 ms in (D, E).

identified by tests similar to those described above. It may be seen that the somata of the claw motoneurones, FCE, SCE and OE, are grouped together in the ganglion (cf. crayfish claw motoneurones, Wiens, 1976). They occur consistently in the triadic relationship shown in Fig. 4 with the FCE being the posterior cell, the SCE the anteromedial cell, and the OE the anterolateral cell. These three cells are the largest ones in the ganglion and form part of a large cluster located in the anterior ventral edge of the ganglion. The FCE has a larger diameter (between 120 and 140 $\mu$m) than the SCE or OE (both of which measure about 100 $\mu$m across). The remainder of the

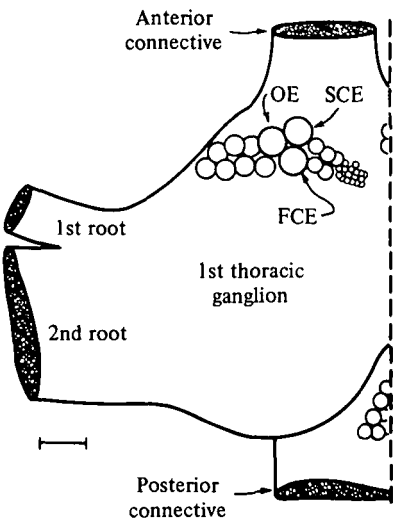


Fig. 4. Ventral view of left half of 1st thoracic ganglion, showing location of FCE, SCE and OE somata in an anteroventral cluster of cell bodies. FCE is larger in diameter than both SCE and OE, which are of similar size. Calibration: 300 μm.

somata in this anterior cluster are smaller than the claw motoneurones. Both in terms of their size and location, the claw motoneurones are easily recognizable from one preparation to the next.

*Physiological asymmetry between FCE and SCE somata*

Following identification of the somata, their responses to sensory stimulation were compared. This was readily done by electrical stimulation of either the 1st or 2nd root (Fig. 2), both of which are mixed roots carrying sensory and motor fibres. The 2nd root was chosen over the 1st root as it was larger and presumably contained more sensory fibres, and as it also evoked a larger response in the somata. For comparative purposes the electrical stimulus applied to the 2nd root was kept constant at 0·2 ms and 50 V. At this setting with external hook electrodes, only sensory elements in the 2nd root were stimulated since no antidromic spikes were seen in the FCE and SCE somata and no orthodromic spikes were seen in their axons.

Table 1. *Asymmetry in spike frequency and burst duration between FCE and SCE somata of cutter and crusher claws, to 2nd root stimulation*

| Spike frequency (Hz) | | Burst duration (s) | |
|---|---|---|---|
| FCE | SCE | FCE | SCE |
| | | Cutter | |
| Nil (EPSP) | 80 | Nil | 1 |
| 1 | 90 | Nil | 1·2 |
| 15 | 70 | 0·02 | 0·08 |
| | | Crusher | |
| 20 | 70 | 0·1 | > 1 |
| 20 | 80 | 0·1 | > 1 |
| 40 | 120 | 0·08 | 1·5 |

Table 2. *Asymmetry in spike frequency and burst duration between homologous (cutter and crusher) pairs of FCE and SCE somata, to 2nd root stimulation*

| | Spike frequency (Hz) | | Burst duration (s) | |
|---|---|---|---|---|
| | Cutter | Crusher | Cutter | Crusher |
| FCE | Nil | 10 | Nil | 0·5 |
| FCE | 1 | 40 | Nil | 0·3 |
| FCE | 10 | 50 | 0·1 | 1·2 |
| SCE | 10 | 50 | 0·8 | 7 |
| SCE | 30 | 120 | 0·5 | > 1 |
| SCE | 40 | 130 | 2 | 15 |

Since the FCE and SCE are known to evoke different types of contraction of the claw closer muscle (Wiersma, 1955; Govind & Lang, 1974), it was not surprising to find a marked difference in the responsiveness of their somata to sensory stimuli. The SCE somata invariably had a higher spike frequency and a longer burst period than the FCE somata (Table 1). For instance, in a cutter claw the FCE soma displayed either an EPSP or at most a single spike in comparison to the SCE soma which produced several spikes (Fig. 5A, B). In a crusher claw the FCE soma produced a couple of spikes compared to many times that number in the SCE soma (Fig. 5C, D).

*Physiological asymmetry between homologous somata*

The properties of homologous somata were compared for homologues from the same animal, following stimulation of the 2nd root with the standard pulse. For both FCE and SCE somata, the crusher side was more responsive than the cutter side, having a higher spike frequency and longer burst period (Table 2). Thus in one preparation 1 spike was seen in the cutter FCE and 7 spikes in its crusher counterpart (Fig. 6A). In another preparation the cutter SCE produced only 3 spikes compared

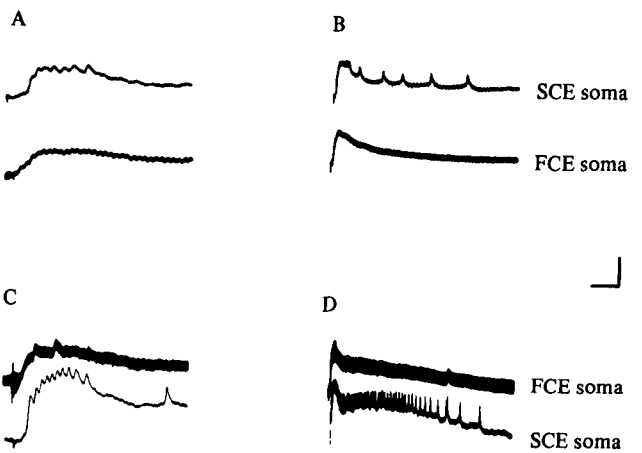


Fig. 5. Physiological asymmetry between FCE and SCE somata to 2nd root stimulation in a cutter (A, B) and a crusher (C, D) claw. The responses are shown at fast (A, C) and slow (B, D) sweep speeds. Vertical calibration: 4 mV in (A, B); 2 mV in (C, D). Horizontal calibration: 40 ms in (A, C); 0·2 s in (B); 0·4 s in (D).

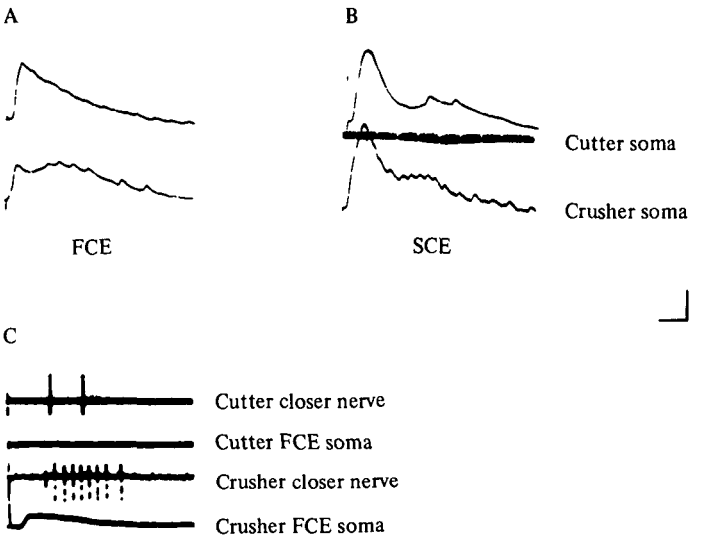


Fig. 6. Physiological asymmetry between homologous FCEs and SCEs to 2nd root stimulation. For each homologous pair, the crusher soma has a greater response than the cutter soma. Vertical calibration: 4 mV in (A, C); 10 mV in (B). Horizontal calibration: 40 ms in (A, B); 20 ms in (C).

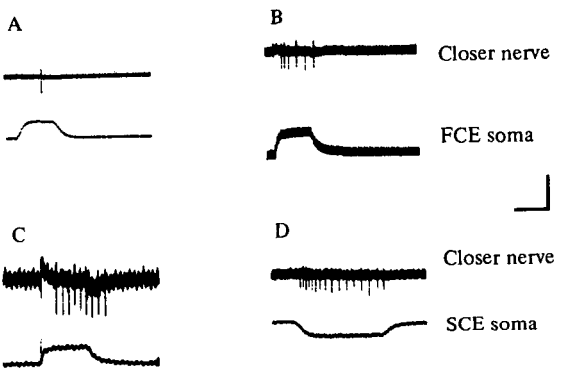


Fig. 7. Physiological asymmetry between homologous FCEs (A, B) and SCEs (C, D) in response to depolarization of the soma. For each homologous pair the crusher soma has a greater response than the cutter soma for a 100 ms depolarizing pulse. Note depolarizing pulse in crusher SCE soma (D) is recorded as a downward deflexion. Vertical calibration: 1 $\mu$A in (B); 2 $\mu$A in (A, C, D). Horizontal calibration: 40 ms in (D); 100 ms in (A, B, C).

to at least 15 spikes on the crusher side (Fig. 6B). In yet another experiment where both pairs of homologous motoneurones could be compared at the same time (Fig. 6C), the cutter FCE did not respond whereas the crusher FCE produced a single soma and axon spike. The SCE motoneurone monitored by its axon showed 2 spikes in the cutter and 8 in the crusher claw.

The responses of homologous somata to current injection were also compared. Fig. 7A, B shows that a depolarizing pulse of 100 ms injected into the FCE soma elicited a maximum of one spike in the cutter claw and six in the homologous crusher claw. The corresponding spike frequencies calculated from these recordings are 10 Hz

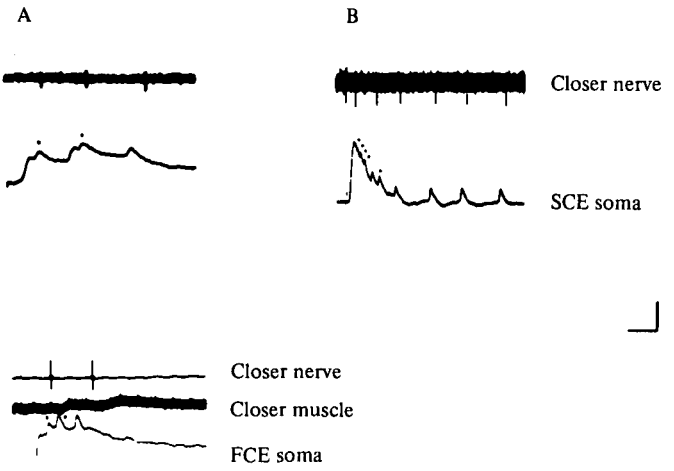


Fig. 8. Physiological asymmetry between soma and axon of FCE and SCE motoneurones to 2nd root stimulation. In all cases the soma shows additional spikes (indicated by dots) compared to its axon. Vertical calibration: 10 mV in (A, B); 4 mV in (C). Horizontal calibration: 40 ms in (A, C); 0·1 s in (B).

for the cutter and 60 Hz for the crusher FCE motoneurones. Similarly depolarization of the homologous SCE somata in another preparation (Fig. 7C, D) elicited 9 spikes in the cutter and 16 in the crusher claws, with the corresponding spike frequencies being 90 Hz and 160 Hz respectively for a 100 ms pulse. These experiments suggest that differences between homologous motoneurones are intrinsic in origin.

*Physiological asymmetry between soma and axon*

In crustaceans, spikes observed in the soma can be attributed to the passive spread of current from a distant spike-initiating zone. Thus, though the spikes in the soma are attenuated, they nevertheless show a 1:1 relationship with spikes in the axon. This relationship was not always observed with the lobster motoneurones. For example, of the 5 spikes produced by an SCE soma (Fig. 8A), only three (1st, 3rd and 4th) had corresponding spikes in the axon; the 2nd and 4th soma spikes had no counterparts at the periphery and they occurred within 10 ms of the 1st and 3rd soma spikes. In another SCE soma the 1st spike had a corresponding axon spike but not the next four, which occurred in the ensuing 30 ms. The 6th soma spike had a matching axon spike but not the 7th, which followed 25 ms later. The subsequent 8th, 9th, 10th and 11th soma spikes all had matching axon spikes. Finally, in an FCE soma, the 1st and 4th spikes, separated by 40 ms, had corresponding axon spikes but not the 2nd and 3rd spikes, which occurred in the intervening period. The failure of spikes to occur in the axon was not related to the interval at which the soma spikes occurred, as this varied from approximately 8 to 25 ms. This is also well beyond the refractory period of axon spikes (Govind & Lang, 1974) and cannot account for the failure of spikes in the axon. Whether this type of asymmetry within an individual motoneurone occurs in intact animals where it might represent an integrative step or in the isolated nervous system is not known.

## DISCUSSION

The triadic grouping of FCE as the posterior cell, SCE as the anteromedial cell and OE as the anterolateral cell, and the large size of these cells, allows them to be identified on the basis of location alone. Their physiological properties and interactions with each other may be examined without having to confirm their identity at the periphery.

The homologous somata in the crayfish are also large cells in the anterior cluster, and they also have a consistent spatial order with each other (Wiens, 1976). However, here the three cells occur in a row proceeding from the midline with the FCE followed by the SCE and finally the OE. Also, in the crayfish the FCE and SCE somata are similar in size, as well as in neurone geometry and dendrite branching patterns.

The FCE and SCE motoneurones of the lobster have a similar physiology to their counterparts in the crayfish. Previous studies have shown that the FCE will cause twitch closing of the claw with one or two spikes whereas the SCE causes closure only with many spikes (Wiersma, 1955; Govind & Lang, 1974), as in the crayfish (Wiens, 1976). The present study showed that the FCE has a higher activation threshold for spike production than the SCE, as in the crayfish (Wiens, 1976).

Both the FCE and SCE somata of the crusher claw are more responsive (i.e. have lower threshold for activation) than their homologues in the cutter claw. Previous studies have revealed that cheliped dimorphism in the lobster encompasses the fibre composition of the closer muscles (Jahromi & Atwood, 1971; Goudey & Lang, 1974; Lang *et al.* 1977; Costello & Lang, 1979) and some neuromuscular properties such as fatigue-resistance of synapses (Govind & Lang, 1974). The differences between homologous FCE somata are in agreement with the contractile behaviour of the claws in intact lobsters. Thus the cutter claw is seen to close completely with a single twitch but not the crusher, which invariably closes slowly. The differences between homologous SCE somata, however, cannot be related to any known difference in the contraction produced by this axon, which is tonic in both claws.

The physiological asymmetry between homologous claw closer motoneurones in the present study was demonstrated primarily by stimulation of sensory elements. Consequently the asymmetry may arise because of differential sensory input or intrinsic differences between homologous motoneurones. However, experiments in which current was injected into the somata also revealed differences in motor output between homologous neurones, thus showing an intrinsic basis for the observed asymmetry. It is, however, possible that extrinsic (sensory) factors are involved.

A peculiarity of the claw closer motoneurones, not in any obvious way related to the dimorphism, was the production of a larger number of spikes in the soma than in the axon. Since the recordings at the periphery were made on the axon before it bifurcates, it is unlikely that conduction failure occurred at any branch points with low safety factors (Parnas, 1972; Grossman, Spira & Parnas, 1973; Hatt & Smith, 1975; Lang & Govind, 1977). Conducation failure must therefore have occurred between the spike-initiating zone in the neuropile of the ganglion and the beginning of the axon at the base of the 2nd root. Whether this spike failure is part of the integration in the neuropile or due to experimental procedure cannot be determined from the existing evidence.

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