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PROJECTIONS OF PRIMARY AFFERENT FIBRES FROM MUSCLE TO NEURONES OF THE SPINOCERVICAL TRACT OF THE CAT

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SUMMARY

1. Micro-electrode recordings were made from axons in the spinocervical tract of decerebrate-spinal cats.

2. The effect of electrical stimulation of afferent fibres in muscle nerves was examined.

3. Stimulation of group III fibres in muscle nerves excited hair only and hair and pressure units in the spinocervical tract. Hair and pressure units also responded to electrical stimulation of group IV fibres.

4. Units of the spinocervical tract excited by stimulation of muscle nerves had receptive fields in the skin overlying the relevant muscles.

5. Stimulation of group III fibres in muscle nerves produced long lasting inhibition of spinocervical tract units. In two such units the inhibitory action of afferent myelinated fibres was enhanced by increasing the stimulus strength so that group IV fibres were recruited.

INTRODUCTION

Many mammalian species possess a sensory pathway in the dorsolateral funiculus of the spinal cord originating in the dorsal horn and ending in the lateral cervical nucleus, the spinocervical tract (Lundberg & Oscarsson, 1961; Taub & Bishop, 1965). Spinocervical tract neurones receive excitatory input from many types of cutaneous receptors (Taub & Bishop, 1965) but not from slowly adapting type I and type II mechanoreceptors, Pacinian corpuscles and rapidly adapting pad receptors (Brown, 1973). With respect to their cutaneous input four different spinocervical tract units can be discriminated in the decerebrate state (Brown, 1971). In the spinal state, where descending inhibition is abolished, the four different types of units are reduced to the following three types: (*a*) units responding to movement of hair but not to pressure applied to the skin (hair only units), (*b*) units responding to hair movement and pressure (h.p. units) and (*c*) a rare type of unit with either no receptive field or a weak response to pressure (Brown, 1971). Because of its powerful input from skin receptors and because of its central connexions, the spinocervical tract is established as a cutaneous sensory pathway (Brown, 1973). However, evoked cortical responses

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in the somatosensory areas S1 and S2 caused by stimulation of high threshold muscle afferents are abolished by section of the dorsolateral funiculus (Norsell & Wolpow, 1966), and spinocervical tract cells may be excited or inhibited from high threshold muscle afferents (Hongo, Jankowska & Lundberg, 1968). The effects of afferent discharge in group IV fibres in muscle nerves were not investigated in these studies.

Recently intra-arterial injections of algesic substances into gastrocnemius and soleus muscles of the cat were shown to produce prolonged responses in the spinocervical tract, and these chemically evoked responses were probably caused by afferent discharge in group III and IV fibres (Kniffki, Mense & Schmidt, 1977). The aim of the present studies was to determine the pattern of projection from muscle afferents to different types of units of the spinocervical tract using electrical stimulation of muscle nerves. The results are consistent with the hypothesis that in addition to its function as a cutaneous pathway, the spinocervical tract is also concerned with afferent activity from receptors in muscle monitoring noxious and possibly other stimuli.

METHODS

Using micropipettes filled with 3 M-NaCl extracellular recordings were made from single fibres in the spinocervical tract of eleven decerebrate adult cats (weight 2·5–3·5 kg), made spinal between C1 and the medulla oblongata. All animals had mean blood pressures of not less than 80 mmHg. The animals were immobilized by I.V. injections of gallamine triethiodide (Flaxedil^{R}) and artificially ventilated with a pump. The end-tidal CO_2 was kept between 3·6 and 4·1 vol. %, and the rectal temperature was maintained close to 38 °C.

Decerebration was performed either by midcollicular section under halothane anaesthesia or anaemically (Borison, Clark & Rosenstein, 1960) under sodium methohexital (Brevimytal^{R}) anaesthesia. No difference was observed between the properties of units of the spinocervical tract in either type of preparation. 3–4 hr elapsed between discontinuing the anaesthetic after decerebration and the first recording.

Laminectomies were performed from C1 to C3 and L1 to L7 vertebrae. Semitendinosus, semimembranosus and the posterior part of biceps were freed in the ipsilateral hind limb, and some or all of the following nerves were prepared for electrical stimulation. Muscle nerves were: hamstring, gastrocnemius and soleus, and femoral nerve; mixed nerve was the common peroneal; and cutaneous nerves were: sural, medial plantar and saphenous. Care was taken to avoid stimulus spread resulting in cross excitation. To minimize this risk, hamstring and gastrocnemius nerves were cut in all experiments and in some the sural. Stimulating electrodes were positioned well away from nerves not to be stimulated. Electrical stimuli of 2 V or less were used to excite myelinated nerve fibres, and with these stimuli cord dorsum potentials were recorded in the appropriate positions. Cross excitation of myelinated nerve fibres could have occurred with strong electrical stimuli necessary to excite group IV fibres. However, this would have been noted because of the short latency of the central response.

The animal was held in a spinal frame, with the head, one thoracic vertebra, the iliac bones and the ipsilateral hind paw firmly fixed. Pools subsequently filled with warm liquid paraffin were formed over the cervical and lumbar cord and over the dorsal aspect of the ipsilateral thigh.

Bipolar ball electrodes for stimulation were placed over the dorsolateral funiculus at C1 and C3 and hook electrodes were positioned at the dissected nerves.

Recordings of the ingoing volley were made with ball electrodes at the appropriate sites of the dorsal cord and electrical thresholds (peripheral) were determined for all nerves on electrodes. During experiments peripheral threshold values were checked repeatedly. Micropipettes were used to record unitary potentials from fibres in the spinocervical tract. Spinocervical tract units were identified by establishing either that a unit did respond to antidromic stimulation from cervical segment C3, but not from C1, or that the conduction velocity was reduced by at least 33 % between C1 and C3 compared with the remaining length of the spinocervical tract fibre (Brown, Hamann & Martin, 1975).

If possible the units were then identified as hair only units, if they responded to movement

of hair with an artists' brush, but not to pressure applied to the skin with a crocodile clip, or as hair and pressure units, if they responded to both types of stimuli.

The receptive field was determined in response to hair movement. All nerves on electrodes were checked for an excitatory response in the spinocervical tract after electrical stimulation with group III, *A* strength (at least 10× nerve threshold) and group IV, *C* strength 20 V, 0·5 msec), and sometimes short repetitive stimuli (max. four stimuli of 50 Hz) were employed. For excitatory muscle nerves the electrical threshold was determined for a response in the tract.

If a unit of the spinocervical tract was inhibited by a volley in myelinated fibres in any of the nerves on electrodes, the inhibitory time course was determined using conditioning volleys caused by stimulation of group III and group IV fibres.

Unitary recordings from the spinocervical tract were fed through a window discriminator, and post-stimulus time histograms assembled with a special purpose computer (Nicolet 1072) were stored on digital tape. With few exceptions eight sweeps were superimposed.

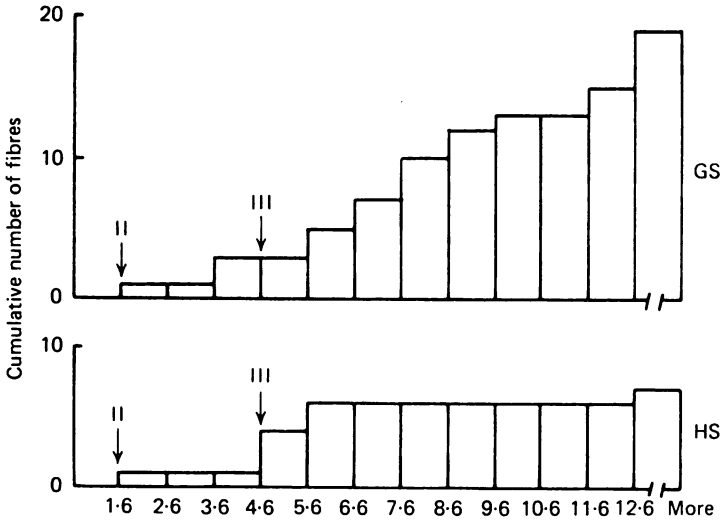

Fig. 1. Cumulative histograms of spinocervical tract thresholds in multiples of peripheral threshold of muscle nerves supplying gastrocnemius-soleus (GS) and hamstring (HS). The arrows indicate electrical thresholds for group II and group III fibres. Only four spinocervical tract units were excitable with stimuli of less than group III strength. For hamstring the thresholds tended to be slightly lower than for gastrocnemius. The sample consists of nineteen units, seven of them excitable from gastrocnemius and hamstring.

RESULTS

Recordings were made from seventy-two single units in the spinocervical tract, forty-nine of which were tested for their excitatory input from cutaneous receptors. Thirty-two units were identified as hair and pressure units (mean c.v. 54 m/sec, S.D. 22·1) and seventeen as hair only units (mean c.v. 75 m/sec, S.D. 31·5). The difference between the conduction velocities of both types of units was significant ($P < 0·025$).

Stimulation of muscle nerves

Forty-two spinocervical tract units could be excited by electrical stimulation of one or more of the muscle nerves on stimulating electrodes. Electrical thresholds were determined for nineteen units excitable either from the gastrocnemius, hamstring

or from both these muscle nerves, which were cut peripherally in all experiments. Fig. 1 gives two cumulative histograms of electrical thresholds for responses in the spinocervical tract in multiples of the electrical threshold for the largest fibres in the same muscle nerve (peripheral threshold). The lowest threshold shown was 1·6 × peripheral threshold, and in 81 % of the tests involving the gastrocnemius or

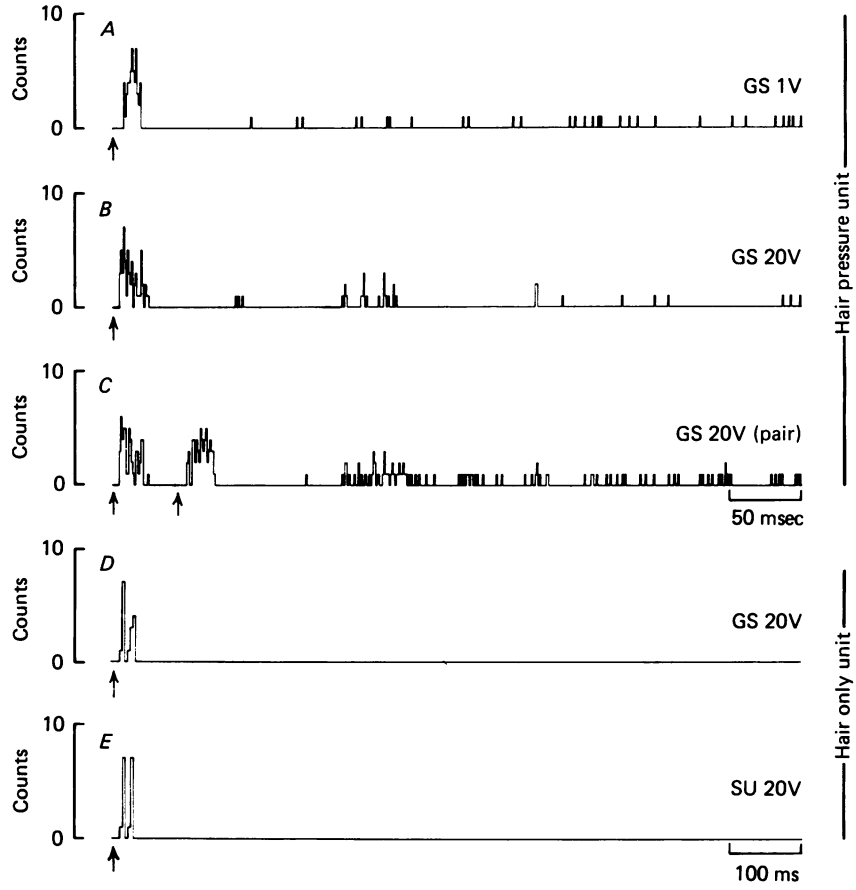

Fig. 2. Effects of muscle afferent volleys on spinocervical tract units. Histograms *A–C* were obtained from a hair pressure unit, *D* and *E* from a hair only unit. In each trace eight responses were superimposed. *A*, response to stimulation of A fibres and resting discharge. *B*, group IV strength stimulus to gastrocnemius-soleus elicits additional long latency response. *C*, double stimulation with group IV strength, enhances the late response. *D* and *E*, stimulation with group IV strength of sural and gastrocnemius only elicits a short latency response in the hair only unit. The electrical threshold for A-fibre in the gastrocnemius-soleus for a response in the spinocervical tract was 1·6 × peripheral nerve threshold. Arrows indicate the timing of electrical stimulation.

hamstring nerve an electrical stimulus of 12·6 × peripheral threshold or less evoked a response in the spinocervical tract. The thresholds for the hamstring tended to be lower than for the gastrocnemius.

60 % of all units tested showed an additional response if the stimulus strength was raised to include the group IV fibres in the muscle volley. The latencies of additional

responses were long enough to allow for conduction in group IV fibres in the respective peripheral nerves.

Electrical stimulation of muscle (three) and skin (seven) nerves produced post-excitatory silent periods (60–370 msec) which were longer than randomly occurring silent periods in seven out of ten spinocervical units. The rates of spontaneous activity ranged from 5·6 to 38 impulses/sec in these ten units.

Natural stimulation of cutaneous receptors and excitation from primary afferent C-fibres

Brown *et al.* (1975) found that hair only units are excitable from cutaneous myelinated fibres, but not from cutaneous non-myelinated fibres, whereas hair and pressure units respond to electrical stimulation of both these types of nerve fibre in

TABLE 1. Relation between cutaneous receptive fields and excitatory muscle nerves. Seven units of the spinocervical tract of this sample were excited from two muscle nerves

	GS nerve is excitatory	HS nerve is excitatory	FE nerve is excitatory	Not excitable by any muscle nerve on electrodes	No. of units
Field over the muscle supplied by excitatory nerve	10	4	5	—	41
Field not over muscle supplied by excitatory nerve	1	1	1	—	
Field not over any muscle supplied by nerves on electrodes	0	0	0	26	

cutaneous nerves. The present results show that this pattern also applies to myelinated and non-myelinated fibres in muscle nerves. For this test all cutaneous nerves had to be left in continuity, the unit had to be excitable from a muscle nerve on electrodes, and the receptive field had to cover areas well away from the pool in the thigh. Twelve units fulfilled all these conditions, and they were tested on their responsiveness to electrical activity in group IV fibres in muscle nerves (Fig. 2). Six units responded to electrical stimulation of group IV fibres in muscle nerves also containing excitatory A-fibres, and five of these six units were of the hair and pressure type. The response to stimulation of group IV fibres was usually potentiated by double shock stimulation. The sixth unit was not tested for a pressure response. The remaining six spinocervical tract units responded to electrical stimulation of A-fibres, but not to stimulation of group IV fibres. The pressure response was doubtful in one unit. One unit was clearly a hair and pressure unit, but it was exceptional in that the cutaneous receptive field did not cover the muscle supplied by the excitatory muscle nerve.

In the present results a pattern was apparent for the spatial relationship between cutaneous receptive fields on individual spinocervical tract units and muscles with afferent fibres excitatory to the same unit. Completely, or in part the cutaneous receptive field tended to be situated over the muscle, stimulation of whose nerve excited the unit under study (Table 1). The figurines in Fig. 3 show all receptive

fields for units excitable from the gastrocnemius in experiments where the sural nerve was not cut. Parts *B–E* of Fig. 3 show completely overlapping fields. In *F–L* the fields covered gastrocnemius–soleus in part and the remaining drawings show receptive fields not overlying gastrocnemius–soleus.

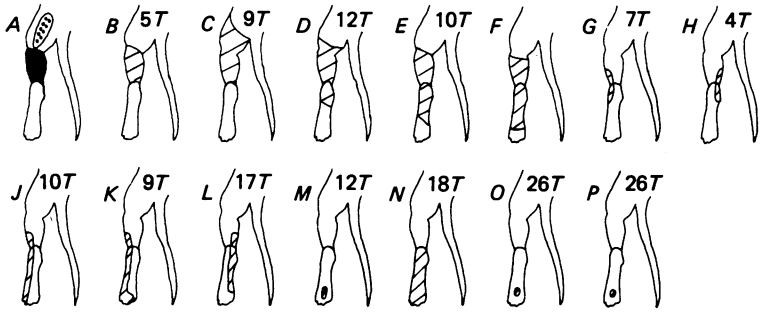

Fig. 3. Cutaneous receptive fields from fourteen spinocervical tract units (*B–P*) excitable from the gastrocnemius. All cutaneous nerves were left in continuity. Where available the thresholds for the gastrocnemius nerve are given as multiples of peripheral thresholds (*T*). *A*, positions of the gastrocnemius muscle (filled) and the pool in the thigh (dotted). In *B–E*, the cutaneous receptive fields cover the gastrocnemius muscle completely, in *F–L* partly, and in *M–P* the gastrocnemius muscle and receptive fields are dissociated. Note the relatively high spinocervical tract thresholds in *M–P*.

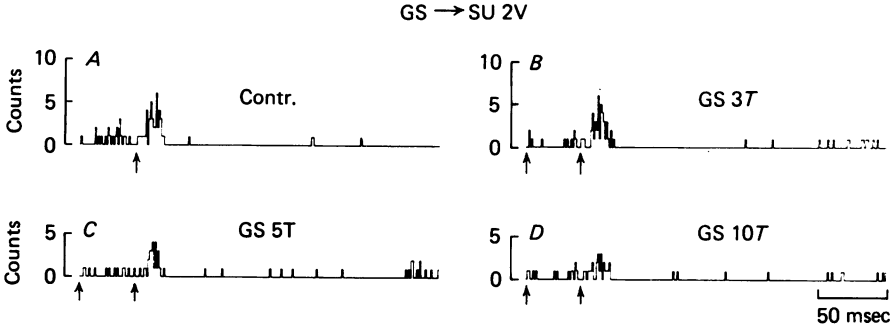

Fig. 4. Inhibition of evoked discharge and resting activity in the spinocervical tract. *A*, control response after 2 V single stimulus to the sural nerve. The stimulus was given with a delay of 40 msec after the trigger pulse to the oscilloscope. In *B–D*, conditioning pulses with increasing stimulus strength were given to the gastrocnemius-soleus nerve at the beginning of the trace. *B*, stimulus strength 3 × peripheral threshold (*T*). *C*, $5 \times T$. *D*, $10 \times T$. Only when the stimulus strength exceeded $3 \times T$ was the evoked response inhibited. Arrows indicate the timing of electrical stimulation.

Inhibition of tract spinocervical units by afferent activity in muscle and skin nerves

Discharge in cutaneous myelinated fibres may produce excitation in one set of spinocervical tract units and inhibition in another (Brown, 1973). In the present investigation, these units were affected in the same way by nervous activity in muscle nerves. The excitatory projections have been described above. Electrical stimulation of myelinated fibres in muscle nerves also produced strong inhibition of responses in the spinocervical tract evoked by stimulation of skin or muscle nerves, and excitatory responses after stimulation of muscle nerves were subject to inhibition as

well (Table 2, Figs. 4*A–D*, 5*A–B*). It appears that afferent activity in group III but not in group I and probably not in group II fibres in muscle nerves produced inhibition of spinocervical tract units. In Fig. 4*B–D*, test responses after stimulation of the sural nerve were preceded by conditioning stimuli to the gastrocnemius–soleus nerve. Only conditioning stimuli of more than 3 times threshold inhibited the test responses. Inhibitory time courses after stimulation of myelinated nerve fibres in

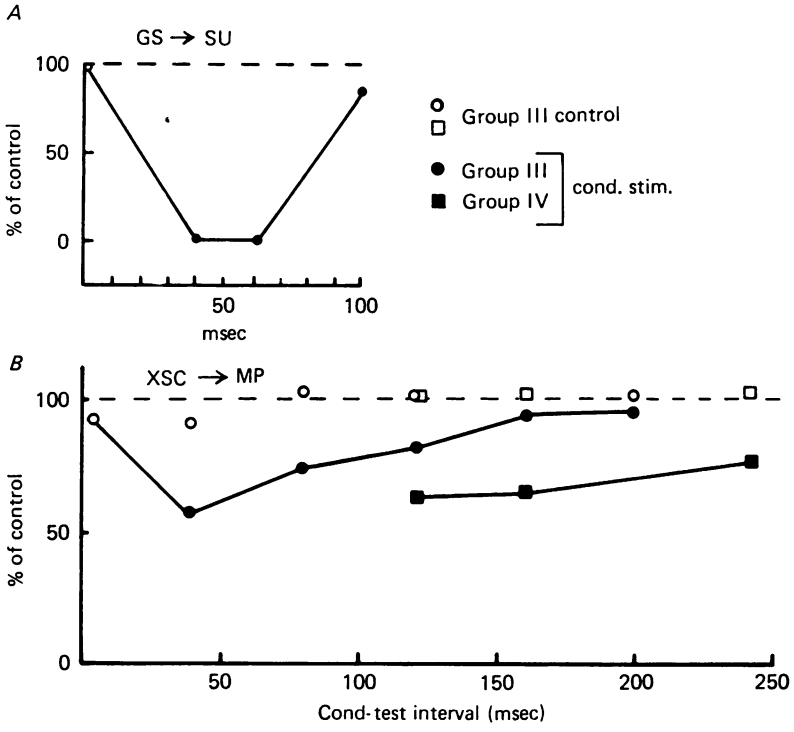

Fig. 5. Time course of segmental inhibition after conditioning stimuli with group III, strength (○, ●) and group IV strength (□, ■). Open symbols stand for control response. Abscissa: conditioning – testing interval. Ordinate: % control response. *A*, conditioning stimuli of 320 mV (4*T*) given to the gastrocnemius-soleus (GS) nerve produced total inhibition of a test response evoked by 700 mV (7*T*) stimuli given to the sural (SU) nerve. *B*, test stimuli of 2 V (22*T*) given to the medial plantar (MP) nerve were preceded by conditioning stimuli of group III strength (2 V, 16*T*) and group IV strength (20 V) given to the contralateral sciatic nerve (XSC). The unit was lost before short conditioning testing intervals could be tested with group IV strength conditioning stimuli. At longer conditioning testing intervals inhibition was enhanced when the strength of the conditioning stimulus was increased from group III to group IV strength.

TABLE 2. Number of spinocervical tract units studied for each permutation of conditioning (giving) and testing (receiving) stimuli. Skin nerve (skin), muscle nerve (muscle), mixed nerve (mixed)

	Giving		
Receiving	Skin	Muscle	Mixed
Skin	4	5	5
Muscle	3	1	2

skin muscle or mixed nerves ranged from 80 msec to values exceeding 200 msec (Fig. 5*A–B*).

Results from four units with conditioning volleys of group I–IV fibres in mixed or muscle nerves were less conclusive. In two units where stimulation of group I–III fibres produced complete inhibition of an evoked response in the spinocervical tract, additional stimulation of group IV fibres in the inhibitory nerve had no effect on strength of duration of inhibition. In the two remaining units, where the groups I and III conditioning volleys reduced the test response to only about 50 %, additional stimulation of group IV fibres (Fig. 5*B*) increased the strength of inhibition at conditioning testing intervals compatible with central actions of discharges in primary afferent group IV fibres.

DISCUSSION

In the present results neurones of the spinocervical tract were shown to be excitable from muscle afferents with spinocervical tract thresholds higher than 1·6 × peripheral threshold. Hair only units were excitable only from myelinated fibres in cutaneous and muscle nerves, whereas hair and pressure units could be excited by electrical stimulation of myelinated and non-myelinated fibres in both types of nerve. Cutaneous receptive fields tended to overlie muscles with afferent nerve fibres excitatory to the same unit. Electrical activity in group III fibres from muscle also caused inhibition of responses in the spinocervical tract.

In previous studies cells in lamina V responded to stimulation of group III muscle afferents (Pomeranz, Wall & Weber, 1968) and spinocervical tract cells could be excited from flexor reflex afferents (Hongo *et al.* 1968). In this investigation the weakest electrical stimulus to elicit a response in a spinocervical tract unit had a strength of 1·6 × peripheral threshold, and only 7·5 % of the units excitable from muscle nerves responded to stimuli of less than 3·6 × peripheral threshold. In a variety of muscle nerves Eccles, Eccles & Lundberg (1957) were able to excite the bulk of group I fibres with electrical stimuli of less than 1·6 × peripheral threshold and 3·6 × peripheral threshold was well beyond the threshold for group II fibres.

In this study 4·6 × peripheral threshold was taken as electrical threshold for group III fibres, because this value lies between the electrical threshold (2·1–3·1 × peripheral threshold) and maximal stimulus (7·3–7·5 × peripheral threshold) for fast γ-fibres in different muscle nerves (mean c.v. 23–32 m/sec) (Boyd & Davey, 1968).

Thus the present findings are in agreement with previous observations (Hongo *et al.* 1968; Pomeranz *et al.* 1968; Brown, 1973) in that group I fibres do not project to the spinocervical tract.

Electrical stimulation of muscle nerves with less than 4·6 × peripheral threshold evoked responses in only 15 % of all spinocervical tract units excitable from muscle nerves, indicating that group II fibres do not have excitatory connexions to the tract to a large extent. All spinocervical tract units excitable from muscle nerves on electrodes responded to stimuli to the respective nerve strong enough to excite group III fibres, and hair and pressure units responded in addition to stimulation of group IV muscle afferents. As only a few muscle nerves were prepared for stimulation, it is likely that all spinocervical tract fibres are excited from muscle nerves in the pattern outlined above.

The present findings obtained with electrical stimulation are in agreement with recent observations using intra-arterial injections of bradykinin, 5-hydroxytryptamine and KCl into skeletal muscle (Kniffki, Mense & Schmidt, 1977). These substances are known to evoke prolonged nervous discharge in group III and group IV muscle afferents, whereas group I and group II fibres are not essentially affected (Mense, 1977). Intra-arterial application of succinylcholine, which is a stimulating agent for primary and secondary endings, only exceptionally produced responses in the spinocervical tract. In conclusion, the present findings are consistent with the hypothesis that the spinocervical tract does not receive excitatory input from primary and probably secondary endings in muscle spindles or from Golgi tendon organs. Receptors in muscle with afferent fibres in group III and IV may be excited by noxious, mechanical, chemical and thermal stimuli (Paintal, 1960; Hertel, Howaldt & Mense, 1976; Kniffki *et al.* 1978). Thus as far as excitatory input from muscle is concerned, the spinocervical tract probably transmits information about noxious and possibly thermal and mechanical stimuli.

Cutaneous receptive fields and muscles giving rise to excitatory nerve fibres for individual spinocervical tract units tended to overlie each other wholly or in part. The same arrangement was observed for cells in lamina V by Pomeranz *et al.* (1968). Similarly, Hagbarth (1957) found the monosynaptic reflex to be enhanced by stimulation of skin overlying the muscle involved. The interpretation of this finding is uncertain.

The earlier finding of Brown *et al.* (1975) that only hair and pressure units are excitable from cutaneous group IV fibres was confirmed in the present work. The new finding is that hair only as well as hair and pressure units are excitable from muscle in afferent groups II–IV. Thus the present results do not support the tentative suggestion of Brown (1973) that hair only units are not excitable from muscle afferents. Furthermore, for individual units of the spinocervical tract, the presence of excitatory input from muscle group IV afferents can be established by checking whether the unit responds to pressure applied to the cutaneous receptive fields.

Afferent input into the spinocervical tract from myelinated nerve fibres in muscle nerves also caused inhibition of evoked responses in the tract by stimulation of muscle skin or mixed nerves. Inhibition of evoked responses was indistinguishable from inhibition after stimulation of skin nerves in its long time course and responses evoked by stimulation of skin or muscle nerves were equally affected. Thus the present findings are in agreement with the model of Brown *et al.* (1975), suggesting presynaptic inhibition at excitatory interneurones as a site for the action of segmental inhibition. In two spinocervical tract units specifically investigated on this point the conditioning stimulus to the inhibitory muscle nerve had to be strong enough to excite group III fibres, before any inhibition was observed. Afferent activity from muscle spindles and Golgi tendon organs does not contribute to segmental inhibition.

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