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# DESCENDING INFLUENCES ON THE RESPONSES OF SPINOCERVICAL TRACT NEURONES TO CHEMICAL STIMULATION OF FINE MUSCLE AFFERENTS

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SUMMARY

1. In cats, extracellular micro-electrode recordings were made from axons of the spinocervical tract (s.c.t.) in both the decerebrate state and during cold block of the spinal cord (reversible spinal state) to examine the effects of intra-arterial injection of algesic agents (bradykinin, potassium, 5-hydroxytryptamine) into the gastrocnemius-soleus (g.s.) muscle on the discharge behaviour of s.c.t. neurones.

2. In the decerebrate state without cooling the spinal cord 13% of the cells (eleven out of eighty-three) responded to intra-arterial injection of bradykinin, 33% (twenty-two out of sixty-nine) to 5-hydroxytryptamine, and 38% (thirty-five out of ninety-one) to potassium injection.

3. The general time course and the latency of the responses of s.c.t. cells induced by injection of pain-producing substances into the g.s. muscle reflect in many respects the activations of g.s. group III and group IV primary afferent units studied previously.

4. For twenty-seven s.c.t. neurones the period of recording was long enough to record the responses of the same cell to injections of algesic agents in both the decerebrate and the reversible spinal state. In the reversible spinal state 83% (nineteen out of twenty-three) of the s.c.t. neurones tested with all the three substances responded to at least one of the algesic agents. In the decerebrate state the percentage was lower (39%).

5. Reversible spinalization led not only to a significant increase in the number of s.c.t. neurones responding to the algesic agents used but also to an increase in the magnitude of the chemically induced responses.

6. The mean latency of the responses of neurones that were activated in both preparations were shorter in the reversible spinal state than in the decerebrate state.

7. Control experiments showed that the responses to bradykinin and potassium were entirely due to the nervous outflow from the g.s. muscle. In contrast, intra-arterially applied 5-hydroxytryptamine influenced the s.c.t. cells via unknown additional sites of action.

8. The results indicate that muscular group III and/or group IV units excitable by algesic substances do project on to neurones of the spinocervical tract. Furthermore it is concluded that the responses of s.c.t. neurones to activation of fine muscle

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afferents by algesic agents are subject to a descending control similar to the well known descending modulation of their responsiveness to cutaneous input. Therefore, in addition to serving as a cutaneous pathway the spinocervical tract may take part in muscular nociception.

## INTRODUCTION

The spinocervical tract (s.c.t.) is a major somatosensory pathway in the dorsolateral spinal afferent system of many mammalian species which originates from cells in Rexed's laminae III, IV and V in the dorsal horn and projects to the ipsilateral lateral cervical nucleus (for a detailed review of the s.c.t., see Brown, 1973).

Using electrical stimulation of peripheral nerves it was shown that the s.c.t. receives cutaneous input from group II and III (Taub & Bishop, 1965) as well as from group IV afferents (Mendell, 1966; Brown, Hamann & Martin, 1975). Although the s.c.t. neurones receive their main excitatory input from cutaneous hair follicle mechano-receptors not subserving a nociceptive function, a portion of them has been shown to carry also information from cutaneous nociceptors (Brown & Franz, 1969; Brown, 1970; Cervero, Iggo & Molony, 1977). Also, using electrical stimulation, an excitatory input from group III muscle afferents on to some s.c.t. cells has been shown to exist by Lundberg & Oscarsson (1961) as well as by Norrsell & Wolpow (1966). An input from muscular group III units to lamina V cells has been reported by Wickelgren (1967) and by Pomeranz, Wall & Weber (1968). More recently and in parallel to the experiments reported here the projection of group III muscle afferents on to s.c.t. neurones has been confirmed, and it has also been shown that electrical excitation of muscle group IV afferents induces discharges in s.c.t. neurones (Hamann, Hong, Kniffki & Schmidt, 1978).

Transmission of somatosensory information via the s.c.t. is modulated by supraspinal control systems (Lundberg, Norrsell & Voorhoeve, 1963; Taub, 1964; Brown & Franz, 1969; Brown, 1971; Brown, Kirk & Martin, 1973; Brown & Martin, 1973; Cervero *et al.* 1977). Similar observations were made on dorsal horn neurones, some of which may send their axons into the spinocervical tract (Wall, 1967; Fetz, 1968; Hillman & Wall, 1969; Besson, Guilbaud & Le Bars, 1975; Handwerker, Iggo & Zimmermann, 1975).

The existing data concerning pain perception from skeletal muscle (Bessou & Laporte, 1958; Paintal, 1960; Iggo, 1961; Franz & Mense, 1975; Fock & Mense, 1976; Kumazawa & Mizumura, 1977; Mense, 1977) indicate that similar to nociception from cutaneous areas, muscle pain is mediated by afferent fibres of groups III and IV. In contrast with the numerous data on the projections of cutaneous group IV fibres on to s.c.t. cells little is known about the projections of muscular group III and group IV fibres on to these neurones.

The present experiments were performed in order to find out whether the s.c.t., in addition to serving as an afferent cutaneous pathway, may constitute an ascending pathway for muscular nociception in the cat. Later the influence of descending spinal pathways on the response behaviour of s.c.t. neurones to algesic chemical stimulation of skeletal muscle was studied. The results show that fine muscle afferents excited by intra-arterial injection of algogenic substances into skeletal muscle project on to cells of the s.c.t. and these projections are subject to a powerful descending inhibitory

control which modulates both the resting activity of the neurones and the activity induced by muscle receptors with fine afferents. Some of the results have been reported (Kniffki, Mense & Schmidt, 1977*a*, *b*).

## METHODS

*General procedures.* The study was carried out on twenty-nine adult cats weighing 1·5–4·0 kg. The animals were anaesthetized with 10–20 mg/kg I.V. sodium methohexital (Brevimytal) after induction with 20 mg/kg I.P. of the same anaesthetic, then an anaemic decerebration similar to the method described by Borison, Clark & Rosenstein (1960) was performed. All animals were immobilized with gallamine triethiodide (Flaxedil, 5–20 mg/kg.hr I.V.) and artificially ventilated. The ventilation volume was adjusted to provide an end expiratory $CO_2$ concentration of 4%. The mean arterial blood pressure was kept above 100 mmHg by infusion of dextran solution if necessary. Occasionally an infusion of dextran solution containing minute amounts of adrenaline was used. The rectal temperature was maintained close to 37·5 °C.

*Preparation.* Two laminectomies were performed to expose the spinal cord, (1) from the first to the seventh lumbar vertebrae and (2) from the first to the third cervical vertebrae. The left hind limb was partially denervated by section of the femoral, saphenous, tibial and hamstring nerves. The sural (su.), common peroneal (c.p.) and gastrocnemius-soleus (g.s.) nerves were exposed for electrical stimulation in continuity. In some experiments all nerves of the hind limb except those supplying the g.s. muscle were sectioned in order to exclude a posible influence from receptors lying in the skin. The animals were rigidly fixed in a spinal frame and over the wounds pools were formed out of skin flaps and filled with warm paraffin oil.

*Recording and identification.* Extracellular recordings were made from single axons of the s.c.t. at the segmental levels $L_3$ and $L_4$ using glass micro-electrodes filled with 3 M-NaCl (initial resistance: 10–20 MΩ). For identification of axons of the s.c.t., the ipsilateral dorsolateral funiculus was stimulated electrically above $C_1$ and below $C_3$. Units were assigned to the s.c.t. if they fulfilled the criteria described by Brown *et al.* (1975). Subsequently the s.c.t. units were tested with electrical stimulation of the peripheral nerves. In those experiments where the su. and c.p. nerves were left intact, hair movement and probing the skin with a glass rod were used as an additional stimulus. It has to be appreciated, however, that the s.c.t. neurones could not be systematically classified according to their cutaneous input characteristics (cf. Brown, 1973), because of the extensive dissection of the hind limb, including a complete denervation in some and at least a partial one in all experiments, and because of the ligation of some cutaneous arteries in order to prevent chemical stimulation of cutaneous receptors. Afferent volleys were monitored with a monopolar platinum ball electrode placed at the dorsal root entry zone to determine the electrical thresholds of the peripheral nerves ($T_p$).

In fifteen experiments a reversible block of the exposed spinal cord first described by Wall (1967) was achieved at the first lumbar segment by means of a cooling thermode similar to the one used by Brown (1971). Blocking was considered complete if the cord dorsum potentials elicited by electrical stimulation at $C_3$ were abolished and the s.c.t. neurone under study could no longer be activated antidromically from the cervical level. The cold block was usually reversible, and so the expression 'reversible spinal state' is used to describe a preparation in which the spinal cord is blocked by cooling.

*Chemical stimulation.* S.c.t. neurones excitable by electrical stimulation of the g.s. nerves were tested by close intra-arterial injection of algesic substances into the gastrocnemius-soleus (g.s.) muscle (for details see Franz & Mense, 1975). Chemical stimulants and their concentrations were bradykinin triacetate (bradykinin 81 μM, potassium chloride (potassium, 0·32 M) and 5-hydroxytryptamine creatinine sulphate (5-HT, 2·5 mM). The injection doses used were: bradykinin 26 μg; potassium, 3·8 mg; and 5-HT, 135 μg. These doses elicit considerable activity in group III and IV primary muscle afferents whereas the mean discharge rate of spindle and tendon organ afferents is not increased (Mense, 1977). To test whether an input via muscle spindle afferents on to s.c.t. neurones was present succinylcholine chloride (0·3 μM) was injected intra-arterially in doses known to elicit strong responses (Granit, Skoglund & Thesleff, 1953; Mense, 1977): SCh, 82–164 μg. Intravenous injections of the test substances into the cephalic vein were performed in order to detect possible actions of the substances outside the g.s. muscle.

*Data processing.* After appropriate amplification and filtering the impulse activity of the s.c.t. neurones was fed through a window discriminator, the output of which was processed on-line by a special purpose computer (Nicolet 1072) which constructed peri-stimulus time histograms of the neuronal discharge.

Quantitative analysis of the chemically induced discharges of s.c.t. neurones was done as follows. The mean resting discharge of a cell in the absence of intentional stimulation was computed by time averaging its activity over a period of 60 sec. The latency of a response was defined as the time from the beginning of the injection to an increase of the discharge of the unit above the mean background discharge before stimulation. The duration of a response was determined as the period during which the impulse activity exceeded the initial mean background discharge level. The Wilcoxon matched pairs signed rank test, the U test of Wilcoxon, Mann & Whitney and the chi-squared test for $2 \times 2$ tables were used for statistical analysis.

## RESULTS

*General properties of s.c.t. neurones.* The data of this study were obtained from ninety-eight neurones of the s.c.t. For twenty-seven cells the period of recording was long enough to study the effects of chemically induced muscle nociceptive input on the same neurone before and during cooling of spinal cord. In the experiments where the su. and c.p. nerves were left intact all but one of the s.c.t. cells had an excitatory receptive field in the skin of the ipsilateral hindlimb. Using a glass rod the locations of the receptive fields were determined before cooling of the spinal cord; most receptive fields were situated distally to the knee joint. No attempt was made to study the ipsilateral or contralateral inhibitory receptive fields.

A background discharge in the absence of intentional stimulation was present in all s.c.t. neurones before and during cooling of spinal cord. The background activity consisted of bursts of impulses separated by silent periods. For the twenty-seven neurones studied in both states the mean background discharge ($\pm$ S.D.) was $8{\cdot}9 \pm 6{\cdot}2$ counts/sec without cooling and $22{\cdot}2 \pm 23{\cdot}4$ counts/sec during cooling of spinal cord (cf. Fig. 2). Out of these twenty-seven neurones seven cells did not change the frequency of their background discharge.

On electrical stimulation of the g.s. nerves the mean s.c.t. threshold ($\pm$ S.D.) was $8{\cdot}6 \pm 7{\cdot}0$ ($n = 70$) times peripheral threshold ($T_p$). In the decerebrate state only four s.c.t. units had a g.s. threshold of less than $1{\cdot}6\ T_p$. For excitation by the c.p. nerve the mean s.c.t. threshold was $1{\cdot}6\ T_p \pm 0{\cdot}6$ ($n = 46$); the mean threshold for the su. nerve was $1{\cdot}9\ T_p \pm 1{\cdot}4$ ($n = 39$). Thus, s.c.t. thresholds for the g.s. nerves were significantly higher than those of the c.p. nerve ($P < 0{\cdot}001$, two-sided test) and of the su. nerve ($P < 0{\cdot}001$). For the su. nerve the s.c.t. thresholds tended to be higher than those of the c.p. nerve, but no significant difference was found. All neurones excitable from the g.s. nerves could be excited from the c.p. nerve. Only a few cells were found which had electrically induced inputs from the g.s. and c.p. nerves but not from the su. nerve. The cumulative relative frequency distribution of s.c.t. cell thresholds for activation from the su., c.p. and g.s. nerves was similar to that found by Hamann *et al.* (1978).

*Effects of algesic chemical stimulation.* In Fig. 1*A* the responses of a s.c.t. cell to intra-arterial injection of the algesic agents and of succinylcholine in a decerebrate cat are shown. Potassium and 5-HT induced high frequency excitations, whereas the administration of bradykinin and succinylcholine had no effect. If a bradykinin response was present as, e.g. in Fig. 2*C* its peak frequency was usually lower than

those of the potassium- or 5-HT-induced responses. The latencies of the responses to administration of 5-HT lay between the potassium-induced and bradykinin-induced responses.

The selective excitatory action of succinylcholine on muscle spindle afferents was used to find out whether, in addition to group III and group IV afferents, Ia and II fibres from skeletal muscle project on to s.c.t. neurones. Compared with the excitations of the algesic agents, especially, potassium and 5-HT, the stimulating effect of succinylcholine was weak; in only three out of twenty units excitations of small magnitude were observed in decerebrate cats without cooling of the spinal cord.

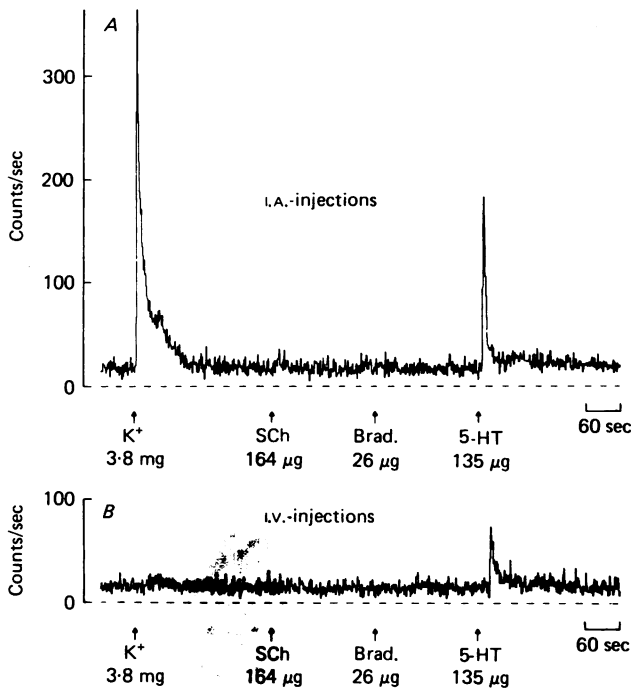


Fig. 1. Comparison of the responses of a spinocervical tract neurone in a decerebrate preparation to intra-arterial (*A*) and I.V. injections (*B*) of bradykinin (Brad.), potassium ($K^+$), 5-hydroxytryptamine (5-HT) and succinylcholine (SCh). Arrows mark the start of the single shot injections which were completed in about 10 sec, dwell time used for the peri-stimulus time histograms was 1 sec.

To make sure that the effects on s.c.t. neurones were due to activation of primary afferents and not to an action outside the g.s. muscle the chemical substances were given intravenously. Of these stimulants only 5-HT had an excitatory effect following intravenous injection (Fig. 1*B*); sixteen out of nineteen s.c.t. cells responded to I.V. administration of 5-HT. Generally this 'centrally' induced response to 5-HT on s.c.t. neurones was smaller and more delayed (mean latency: $20{\cdot}3 \pm 13{\cdot}5$ sec) than that following 5-HT injection into a g.s. muscle artery. Although it might be possible in most cases to recognize a peripherally induced effect of 5-HT by its short latency, the duration and the magnitude was not determined because of the overlap with the 'centrally' induced responses. In some experiments additional direct evidence for a

muscular site of action of the algesic agents was obtained by cutting the g.s. nerves after a response of a s.c.t. unit to e.g. bradykinin had occurred. The response to the algesic agent was abolished after cutting the g.s. nerves (the cutting itself induced a short burst of impulses but did not change the background discharge appreciably).

Cooling of the spinal cord markedly enhanced the responsiveness of the s.c.t. neurones to algesic chemical stimulation of the g.s. muscle. In Fig. 2*A* the discharge of a neurone is shown which did not respond to administration of bradykinin, potassium and 5-HT before cooling of the spinal cord, but during cooling of the cord

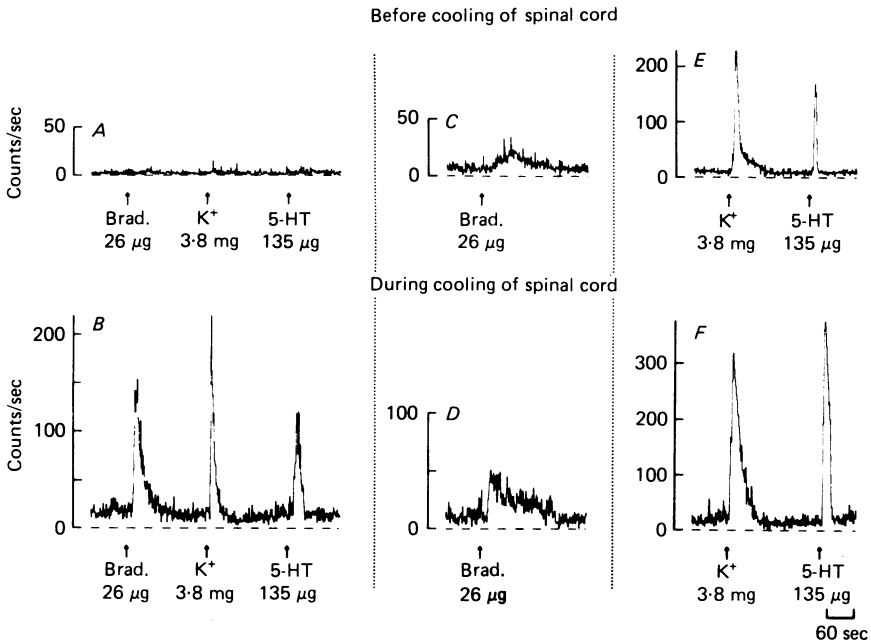


Fig. 2. Responses of three spinocervical tract neurones to algesic chemical stimulation of the gastrocnemius-soleus muscle in decerebrate cats before cooling of spinal cord (*A*, *C*, *E*) and the responses of the same cells during cooling of spinal cord (*B*, *D*, *F*). The algesic agents (Brad.), potassium ($K^+$) and 5-hydroxytryptamine (5-HT) were injected into the arterial circulation of the g.s. muscle at the arrows. The histograms were constructed with a dwell time of 1 sec; temperature of the cooling thermode: −1 °C.

all three substances induced a clear excitation (Fig. 2*B*). Some of the s.c.t. neurones responded to at least one of the chemical stimulants in the decerebrate state before cooling. In Fig. 2*C*, *D* the enhancement by cooling of the cord of a bradykinin-induced response is shown and in Fig. 2*E*, *F* a similar enhancement for the responses to potassium and 5-HT for another s.c.t. cell is illustrated.

*Effectivity of the chemical stimuli.* In the decerebrate state without cooling the cord 13 % (eleven out of eighty-three) of the s.c.t. neurones were excited by injections of bradykinin. Following the injection of potassium, 38 % (thirty-five out of ninety-one) of the s.c.t. cells showed on increased activity; injections of 5-HT induced excitatory effects in 33 % (twenty-two out of sixty-nine) of the neurones.

To study quantitatively the influence of the descending control by cooling of the

spinal cord, in the following only those twenty-seven cells were taken into account for which the period of recording lasted long enough to study the chemically induced effects on the same neurone before and during cooling of the cord. Among the stimulants used potassium was the most effective one. The percentage of neurones responding to the various agents in both states is shown in Fig. 3. For bradykinin and potassium the increase in the percentage of neurones responding during cooling of the spinal cord was the same (37 %) at an equal level of significance ($P < 0{\cdot}01$; two-sided test). The percentage of s.c.t. neurones responding to administration of 5-HT was also higher during cooling, but the difference was not significant.

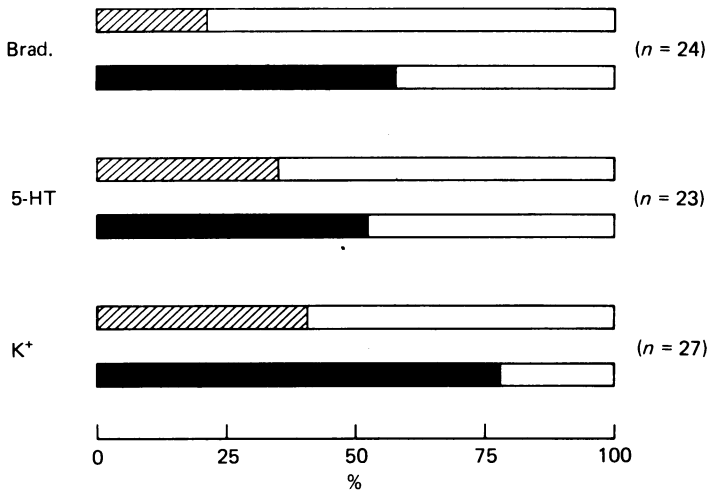


Fig. 3. Effectiveness of the chemical stimuli in the decerebrate and in the reversible spinal preparation. The bars indicate the percentage of s.c.t. neurones which responded to injections of the test substances bradykinin (Brad.), potassium ($K^+$) and 5-hydroxytryptamine (5-HT). Hatched bars: decerebrate state; filled bars: reversible spinal state. The number ($n$) of cells tested with the respective substance is given at the right side.

Out of the twenty-seven cells recorded from in both states, twenty-three were tested with all three algesic agents (bradykinin, potassium and 5-HT). The distribution of these cells for the various response combinations is shown in Fig. 4. Four units responded to all three stimulants in the decerebrate preparation, whereas in the reversible spinal state nine neurones showed such a response behaviour (Fig. 3*A*, *C*). No response to any of the applied substances was present in 14 of the twenty-three cells in the decerebrate state; during cold block of the spinal cord this number decreased to 4. In Fig. 4*B*, *D* the response combinations to all three, to two and to one substances are summarized. During the reversible spinal state 83 % (nineteen out of twenty-three) of the s.c.t. neurones responded to at least one of the stimuli; this percentage decreased to 39 % (nine out of twenty-three) in the decerebrate state.

*Quantitative evaluation of the response.* Between individual spinocervical tract neurones the latency and time course of the excitation following injection of a particular algesic agent varied. Yet certain features of the responses were in some way characteristic for the effect of the respective stimulant. The latency, duration and magnitude of the responses of s.c.t. neurones to injections of the various stimulants

are listed in Table 1. In columns *A* and *B* the values for cells responding in the decerebrate as well as in the reversible spinal state are given. In column *C* the responses of those units are listed which were responsive in the reversible spinal state only. As can be seen from this Table, the responses to injections of bradykinin had the longest latency followed by the latencies of the responses to 5-HT and then to potassium. Comparing the latencies of the responses of neurones listed in column *B* and column *C* of Table 1, the mean latency for cells responding only in the reversible spinal state appears to be longer than the mean latency of units responding in both states. For the effects of potassium this difference was statistically significant ($P < 0{\cdot}02$, two-sided test).

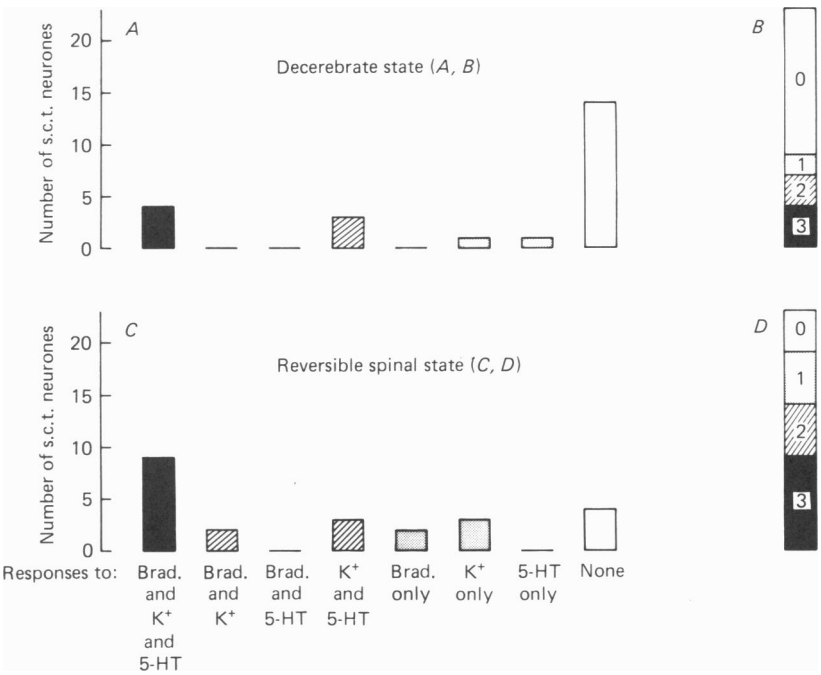


Fig. 4. Response combinations of spinocervical tract neurones to chemical stimulation of gastrocnemius-soleus afferents in the decerebrate (*A*, *B*) and reversible spinal state (*C*, *D*). The results were obtained from twenty-three s.c.t. neurones which were tested with all the substances used (Brad., $K^+$, 5-HT). The columns *B* and *D* summarize the data shown in *A* and *C*, respectively. They indicate in a cumulative way the number of cells which responded to all three substances (3), two substances (2), one substance (1), or none of the stimulants (0).

With regard to the magnitude of the evoked responses three features deserve mentioning: (1) despite the different time course of the bradykinin- and potassium-induced responses, their magnitudes (counts/ response)were similar in each of the two states (compare within *A*, *B*, *C*), (2) the magnitudes were significantly greater in the reversible spinal state than in the decerebrate state (bradykinin, $P < 0{\cdot}01$; potassium, $P < 0{\cdot}02$, one-sided test; compare *A* with *B*), and (3) the magnitude of response of neurones only being activated in the reversible spinal state was lower than that of cells which were excited in both states (bradykinin, $P < 0{\cdot}05$; potassium, $P < 0{\cdot}10$, two-sided test; compare *B* with *C*).

## DISCUSSION

The results of this study indicate that many s.c.t. neurones receive an excitatory input from fine muscle afferent fibres but none or almost none from muscle spindle or Golgi tendon organ afferents. Several lines of evidence support this conclusion: first of all, chemical algesic stimulation as used here almost selectively excites muscle group III and IV afferent units (Mense, 1977). Secondly, the responses of the s.c.t. cells to such stimuli correspond in general to the patterns of activation of these afferents (cf. Fock & Mense, 1976; Mense, 1977), except that the increase in firing rate of the

TABLE 1. Quantitative evaluation of the responses of spinocervical tract neurones to injections of algesic agents into the g.s. muscle

| Feature | Agent | Units responding in the decerebrate (*A*) and in the reversible spinal state (*B*) | | Units responding only in the reversible spinal state |
|---|---|---|---|---|
| | | *A* | *B* | *C* |
| Latency (sec) | Bradykinin | 22·1 ± 11·4 ($n$ = 7) | 11·9 ± 5·2 ($n$ = 7) | 16·2 ± 11·1 ($n$ = 7) |
| | $K^+$ | 4·4 ± 1·3 ($n$ = 11) | 4·0 ± 1·8 ($n$ = 11) | 7·9 ± 3·8 ($n$ = 10) |
| | 5-HT | 6·9 ± 3·5 ($n$ = 8) | 8·3 ± 4·6 ($n$ = 8) | 9·2 ± 5·0 ($n$ = 4) |
| Duration (sec) | Bradykinin | 91·6 ± 26·8 | 86·6 ± 57·3 | 93·4 ± 44·7 |
| | $K^+$ | 53·5 ± 20·2 | 57·1 ± 21·2 | 57·3 ± 21·8 |
| Magnitude (counts/ response) | Bradykinin | 771 ± 414 | 2409 ± 672 | 1172 ± 765 |
| | $K^+$ | 1138 ± 1068 | 2211 ± 1893 | 955 ± 741 |

For determining the magnitude of an excitatory response the activity following an injection was integrated over the period of response; from the integral the background discharge prior to the injection was subtracted. Duration and magnitude of the 5-HT-induced effects were not determined because of the possible interference with 'centrally' induced activations. All values are given in mean ± S.D.; the number of neurones used for calculating latency period, duration and magnitude of the responses are given in parentheses.

central neurones is much greater than that of the afferents (i.e. the activity generated by the afferents is amplified in the central pathway). Thirdly, injections of succinylcholine have very little effect upon the activity of s.c.t. cells despite the fact that the same dose of succinylchlorine produces powerful excitations of group Ia afferents (cf. Granit *et al.* 1953; Mense, 1977). Lastly, as shown in more detail in the comparison investigation (Hamann *et al.* 1978), the strength of electrical stimulation of the g.s. nerve usually has to be increased to several times that for groups I and II before s.c.t. neurones are activated.

We did not observe clear inhibitory effects on the discharge of spinocervical tract neurones following administration of bradykinin, potassium or 5-HT. For bradykinin, clear inhibitory effects have been reported by Besson, Conseillier, Hamann & Maillard (1972) as well as by Besson, Guilbaud & Le Bars (1975) in their studies of the discharge of cells situated in lamina V. Besides the fact that only part of the lamina V cells project into the s.c.t., a possible explanation for this difference might be that in the experiments of the above mentioned authors the chemical stimulation induced a mixed input from cutaneous as well as from muscular receptors. Furthermore, using the horse radish peroxidase method it has recently been shown that the majority of

labelled s.c.t. cells were located in the ipsilateral laminae IV throughout the spinal cord (Craig, 1976). Thus, it might be that only a part, if any, of the lamina V cells project into the s.c.t. In addition, it has to be kept in mind that in the present study only those s.c.t. units were tested with chemical stimulation of the g.s. muscle which were excited by electrical stimulation of g.s. afferents.

In the reversible spinal state the background activity of the s.c.t. cells is much greater than in the decerebrate preparation. This finding is in good agreement with the observations of Wall (1967), Besson *et al.* (1975), Handwerker *et al.* (1975), Le Bars, Menetrey & Besson (1976) on dorsal horn neurones, and those of Brown (1971) and of Cervero *et al.* (1977) on spinocervical tract cells. Conjointly with the increase in background frequency the effectiveness of the chemical algesic stimulation increases in the reversible spinal state. This is taken to indicate that the discharges of s.c.t. neurones induced by activity in fine muscle afferents are modulated by descending control systems similar to or identical with those operating on the responses of these cells to cutaneous input (cf. Brown, 1973; Cervero *et al.* 1977). Probably due to the different input pattern induced on to s.c.t. cells by administration of potassium and bradykinin, potassium was more effective than bradykinin. But for both agents the increase of the percentage of neurones responding to the two agents was the same (37%). As far as the bradykinin-induced responses are concerned this observation is well in agreement with the findings of Besson *et al.* (1975), Le Bars *et al.* (1977) on lumbar lamina V dorsal horn cells.

The powerful descending control is also revealed by the fact that the responses of the s.c.t. neurones were larger and their mean latency shorter in the reversible spinal state than in the decerebrate preparation. Individual s.c.t. cells seemed to be affected differently by the descending control as particularly revealed by those cells which respond only in the reversible spinal state (Table 1*C*). Cells with a low background discharge rate in the decerebrate state are subject to the most powerful descending influence in agreement with results of Cervero *et al.* (1977) for the s.c.t. cells described as E-cells.

In the reversible spinal state 83% of the neurones responded to at least one of the algesic agents applied. In the decerebrate preparation this percentage decreased to less than 40%. To assess the importance of the s.c.t. in muscular nociception of free living animals one has to keep in mind that the relatively low value of less than 40% may underestimate the units responding to at least one of the chemicals since it is known that other spinal processes are inhibited to a larger extent in decerebrate than in intact preparations. In addition to the high threshold muscle input the s.c.t. neurones also receive a powerful input from the skin. Due to this convergence of information on to the same cell, parallel processing of the peripheral information in different ascending pathways is probably required to enable higher centers to discriminate between noxious and nonnoxious stimuli to muscle and skin. The descending control systems may take part in this discrimination. However, the detection and discrimination problem is admittedly far from being solved. There is a remarkable parallel between the findings of this report and its companion one (Hamann *et al.* 1978) and those results which have beeen obtained when studying the afferent input from muscle into primate spinothalamic tract cells (Foreman, Kenshalo,

Schmidt & Willis, 1979*a*; Foreman, Schmidt & Willis, 1979*b*). For instance, the majority of spinothalamic cells had a convergent input from cutaneous as well as from high threshold muscle afferents, whereas electrical or chemical excitation of low threshold muscle afferents was usually ineffective. Because of these and many other similarities it has been proposed that the spinothalamic tract of the primate and the spinocervical tract of the carnivore share comparable functions (Foreman *et al.* 1978*b*). It has to be appreciated, however, that a more detailed assessment of their functional overlap as well as any estimate on their role in transmitting muscle nociception requires a much better understanding of the mode of operation of these and other spinal sensory tracts.

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