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AN INTRACELLULAR STUDY OF DESCENDING AND NON-CUTANEOUS AFFERENT INPUT TO SPINOCERVICAL TRACT NEURONES IN THE CAT

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SUMMARY

1. Previous studies of input on to spinocervical tract neurones have been extended by investigating the post-synaptic actions of non-cutaneous afferent fibres and of descending tracts on to these neurones, using intracellular recording. In particular, actions of group II muscle, joint and Pacinian afferent fibres and rubro- and corticospinal tract fibres were investigated.

2. Group II muscle afferent fibres evoked excitation and inhibition at a minimal latency compatible with a disynaptic linkage. Increasing the stimulus strength to include group III afferent fibres enhanced these post-synaptic actions only modestly. Inhibition was evoked less frequently and/or required trains of stimuli.

3. Weak stimulation of the interosseous nerve evoked short latency (disynaptic) inhibition or excitation, the latter less frequently. Post-synaptic potentials evoked below threshold for group III afferent fibres of the interosseous nerve are attributed to the actions of Pacinian corpuscles.

4. Low threshold joint afferent fibres evoked excitation at short latency. Higher threshold joint afferent fibres usually evoked inhibition at longer latency, although high threshold excitation was sometimes observed.

5. Stimulation of the pyramidal tract evoked constant latency, unitary e.p.s.p.s which followed high frequencies. The evidence suggests that such e.p.s.p.s are evoked monosynaptically. Polysynaptic excitation and inhibition were also observed.

6. No convincing evidence could be found of actions evoked directly by the rubrospinal tract, although actions mediated via other descending systems could be induced from the red nucleus.

7. A large degree of convergence was seen from different peripheral and descending systems on to individual neurones.

INTRODUCTION

The spinocervical–lemniscal pathway is one of the major routes by which tactile information reaches the cerebral cortex (for references see for example Brown, 1981*a*). Neurones of the spinocervical tract (s.c.t.) are nevertheless influenced by both

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non-tactile as well as tactile stimuli. They are most powerfully activated from hair follicle receptors (for review see Brown, 1981*a*, *b*) but are also affected by other receptors, such as nociceptors (see for example Cervero, Iggo & Molony, 1977; Kniffki, Mense & Schmidt, 1977) and by various receptors whose afferents course via joint, interosseous and muscle nerves (Hongo, Jankowska & Lundberg, 1968; Hamann, Hong, Kniffki & Schmidt, 1978). Since actions from non-cutaneous receptors have been investigated in a much less extensive way than actions from cutaneous receptors, one aim of the present study was to extend the study of input from joint, interosseous and group II muscle afferent fibres to s.c.t. neurones. A second aim was to acquire information regarding the actions of the rubrospinal and corticospinal tracts because, while it is well established that s.c.t. neurones are under descending control, the mechanism of this control and the identity of the descending pathways involved are largely unknown.

The input to s.c.t. neurones has been investigated with intracellular recording to allow us to define the post-synaptic actions of the fibre systems under study and to detect small post-synaptic potentials which might have been missed with extracellular or axonal recording. A preliminary report of some of these results has appeared (Harrison & Jankowska, 1984).

METHODS

Preparation

Cats were anaesthetized with chloralose (initial dose 50–60 mg/kg after ether anaesthesia during surgery, followed by two or three supplementary doses of 10–20 mg/kg). The cats were paralysed with gallamine triethiodide (May and Baker) and artificially ventilated. Deep anaesthesia was assured by observations of pupil diameter and from observations of adequate anaesthesia of non-paralysed animals during other experiments with an identical anaesthetic regime. End-tidal CO_2 was kept at about 4 % and the blood pressure above 90 mmHg. The following hind-limb nerves were dissected, cut and prepared for stimulation: anterior biceps–semimembranosus, posterior biceps–semitendinosus, gastrocnemius–soleus, plantaris, flexor digitorum longus, popliteus, deep peronei (anterior tibial and extensor digitorum longus), tibial, sural, the cutaneous branches of superficial peroneal, posterior joint and interosseous. Laminectomies exposed the spinal cord at C1, C3, Th13 and from L3 to sacral segments. Craniotomies exposed the dorsal part of the parietal lobe and the caudal part of the cerebellum in order to stimulate the red nucleus and the pyramids respectively. The dorsal columns were sectioned at Th13 level to avoid any complications due to spread of current to them. This alleviated any possible ambiguities in the identification of s.c.t. neurones by either synaptic activation of s.c.t. neurones or antidromic activation of neurones with an axon in the dorsal columns. Pairs of silver electrodes were placed on the surface of the ipsilateral dorsolateral funiculus at C1, C3 and Th13 segments.

Stimulation and recording

Neurones were selected while tracking through the dorsal horn within the region with a large field potential from cutaneous afferents. In searching for spinocervical tract neurones, electrical stimuli were applied to the lateral funiculus at Th13 (with 0·5–1·0 mA, using two electrodes in contact with the surface of the spinal cord) until an antidromic action potential was recorded extracellularly. The presence or absence of an ascending axonal projection to the cervical segments was established by observing whether or not the cell was antidromically activated following stimulation of the lateral funiculus at the C3 and C1 segments (with stimulus strengths of up to 1·5 mA). Cells were classified as s.c.t. neurones if there was no antidromic response from C1, or if the threshold for antidromic activation from this site was substantially higher than that from C3. In the latter case activation was attributed to stimulation of a thinner ascending axon collateral within the C1 segment, or to current spread to the C3 level. An attempt was then made to penetrate

the neurone, either in the same or in another electrode track. Intracellular recordings were made with potassium-citrate-filled electrodes with tips broken to give impedances of 3–5 MΩ. Smaller electrodes would have been less damaging but, in view of the higher resistance, their use considerably limited the possibilities of tracking for the chosen neurones. After penetration it was verified that the cell was antidromically invaded and excited by cutaneous afferent fibres. Thereupon, the input from all the available fibre systems was tested. Intracellular recordings were taken simultaneously with recordings from the surface of the spinal cord so that the latencies of p.s.p.s could be measured with respect to the arrival of afferent or descending volleys. Recordings taken just outside the cells were used to differentiate between field potentials and genuine p.s.p.s. Most of the data were recorded as single sweep records but were often supplemented by averaged records of typically 512 (but sometimes up to 2048) single sweeps for each average.

Primary afferent fibres (cutaneous, muscle, joint and interosseous afferents) were activated by electrical stimulation of peripheral nerves from one to twenty times threshold for the lowest threshold fibres. Single stimuli or trains of two to five stimuli were used.

Corticospinal tract fibres were stimulated within the contralateral pyramid at the level corresponding to the rostral part of the inferior olive, as subsequently verified histologically. The pyramid was stimulated monopolarly with a tungsten electrode inserted through the cerebellum, at an angle of 35 deg from the vertical, aiming at Horsley-Clarke location P 8–10, L 0·8–1·0, H − 10. The position of the electrode was adjusted while recording the actions of stimuli applied through the electrode. The electrode position was considered satisfactory when descending volleys recorded from the surface of the lateral funiculus at Th12–13 appeared with a stimulus strength of 10–20 μA and were maximal or near maximal with a stimulus strength of 100 μA. Single stimuli or trains of stimuli (0·1 ms duration and up to 100 μA) were used.

Rubrospinal tract neurones were activated directly and/or trans-synaptically (Baldissera, Lundberg & Udo, 1972). The stimuli were applied within the caudal part of the contralateral red nucleus, usually at its ventral border as verified histologically. The placement of the electrode was as described by Hongo, Jankowska & Lundberg (1969). Stimuli with the same parameters as for pyramidal stimuli were used.

RESULTS

The reported observations are based on intracellular records from a sample of thirty-four spinocervical tract neurones in L6 and L7 segments. All of the observations to be reported were made on s.c.t. neurones (twenty-two) which were antidromically activated from C3 but not from C1. A number (twelve) of neurones with a possible collateral projection to C1 (see above) were nevertheless included in the present sample since such neurones have previously been considered to be s.c.t. neurones but project, in addition, rostrally to other structures (see for example Brown & Franz, 1969; Brown, 1971, 1981*a*, *b*; Dart & Gordon, 1973; Craig & Tapper, 1978). On the basis of the present intracellular recordings this latter group appeared indistinguishable from those that terminated in C2–3.

Cutaneous afferent fibres

The projection of cutaneous afferent fibres to s.c.t. neurones was not the main aim of the present study, though the actions of cutaneous afferent fibres were recorded routinely. These were essentially as described in previous intracellular studies. Thus, all s.c.t. neurones encountered were monosynaptically excited from the lowest threshold cutaneous afferent fibres, and post-synaptic inhibition was often evoked both from the nerve which evoked the excitation and from other cutaneous nerves stimulated (Hongo *et al.* 1968; Hongo & Koike, 1975). Most of the present sample of neurones were monosynaptically excited from the superficial peroneal nerve (which

was generally the most effective source of input) and often inhibited from the sural nerve.

The finding that most of the units in the present sample were inhibited by the sural nerve is of interest in relation to the observations of Taub & Bishop (1965) that the lowest threshold fibres in the sural nerve do not excite s.c.t. neurones. This may either reflect a sampling bias in both their and our studies, or reflect the fact that the toes and distal part of the foot (from which a high proportion of s.c.t. neurones are activated) are not innervated by the sural nerve.

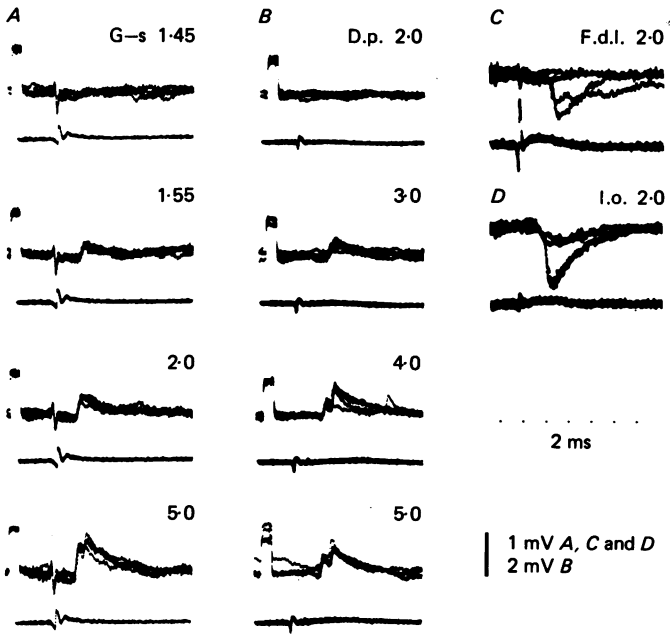

Fig. 1. The action of group II afferent fibres of gastrocnemius–soleus (G–s) muscle (*A*), of the deep peronei (D.p.; *B*) and of flexor digitorum longus (F.d.l.; *C*) upon three s.c.t. neurones. Records in *D* show, for comparison, i.p.s.p.s evoked from the interosseous nerve (I.o) in the same neurones as those in *C*. Note similarly unitary character of these i.p.s.p.s but at longer latency when evoked from F.d.l. Upper traces, intracellular records of p.s.p.s. Lower traces, cord dorsum potentials. The stimulus intensities above each set of records are in multiples of thresholds for group I fibres. The voltage calibration is for intracellular records.

Muscle afferent fibres

The lowest threshold actions evoked by stimulation of muscle nerves always required stimuli above 1·5 times threshold for the lowest threshold fibres. Since this corresponds to the lowest threshold group II fibres (Jack, 1978), it would appear that group I fibres have no action on s.c.t. neurones and hence confirms previous studies (Hongo *et al.* 1968; Hamann *et al.* 1978). Some of the lowest threshold excitatory post-synaptic potentials (e.p.s.p.s) detected are illustrated in Figs. 1 *A* and *B* and 3 *B*. The latencies for such e.p.s.p.s ranged from 3·5 to 7·0 ms measured from the stimulus, and from 1·6 to 4·5 ms measured from the arrival of the group I volley at the cord

dorsum. According to Fu, Santini & Schomburg (1974), 70 % of monosynaptic focal potentials from group II afferent fibres in the dorsal part of the grey matter occur at latencies of 3·1–3·3 ms measured from the gastrocnemius–soleus stimulus. The latencies (measured from the stimulus) of e.p.s.p.s evoked by gastrocnemius–soleus group II afferent fibres of the present data were 3·8–4·2 ms. Thus it is likely that the difference in latency is due to an additional single synapse, making the minimal linkage between group II afferent fibres and s.c.t. neurones disynaptic. This is entirely compatible with the latencies of group II e.p.s.p.s evoked in motoneurones and attributable to a disynaptic linkage (see for example Lundberg, Malmgren & Schomburg, 1975). Increasing the stimulus strength from five to twenty times threshold, to recruit the higher threshold group II and the group III fibres, only moderately enhanced the group II e.p.s.p.s, although quantitative assessments were difficult when longer latency p.s.p.s (Hongo *et al.* 1968) followed stronger stimuli. Excitatory actions of group II muscle afferents were evoked by single stimuli in fourteen neurones.

Inhibitory actions of single stimuli (with intensities up to five times threshold) were less frequent. They were seen in six neurones while in four neurones the i.p.s.p.s appeared only upon the second or third stimulus. However, despite the apparently weaker coupling in the inhibitory pathways, the latencies of the i.p.s.p.s (1·8–4·5 ms from the arrival of the relevant group I volley) indicated a similar number of interposed interneurones. The most distinct i.p.s.p.s, those with the shortest latencies, were evoked from the flexor digitorum longus nerve. They are illustrated in Fig. 1*C* with records at threshold for the i.p.s.p.

Interosseous afferents

Since group I afferent fibres have no action on s.c.t. neurones and since afferent fibres of Pacinian corpuscles constitute virtually the whole of the group II component of the interosseous nerve (Boyd & Davey, 1968), electrical stimulation of this nerve could be used to determine any action of Pacinian corpuscles upon the spinocervical tract. In a previous study, one s.c.t. neurone was reported to be inhibited upon stimulation of the interosseous nerve and four neurones were inhibited upon stimulation of the flexor digitorum longus nerve when it included the interosseous nerve (Hongo *et al.* 1968). All five neurones were inhibited at short latency.

In the present study, weak stimulation of the interosseous nerve evoked short latency inhibition in twelve neurones. An example of this with graded stimulation of the interosseous nerve is shown in Fig. 2. The threshold for the i.p.s.p. was similar to the threshold expected for activation of Pacinian afferents (Yeo, 1976) and the amplitude of the i.p.s.p. increased in parallel with the negative cord dorsum potential which follows the group I volley at short latency. This cord dorsum potential has been attributed to the action of Pacinian afferent fibres (Harrison & Johannisson, 1983) and such parallel growth of this potential with the amplitude of the i.p.s.p. is consistent with its Pacinian afferent fibre origin. The negative cord dorsum potential is shown more clearly with the use of averaging in Fig. 2*B*. As a further control that the short latency inhibition and the negative cord dorsum potential are due to the action of Pacinian afferent fibres, activation of the nerve to flexor digitorum longus (which is closely associated with the interosseous nerve: see Hunt & McIntyre, 1960;

Harrison & Johannisson, 1983) did not evoke these actions even at five times threshold. The latency of the inhibition in this example was 2·1 ms (measured from the group I volley) and ranged from 1·5 to 2·4 ms in different neurones. This is compatible with the disynaptic linkage originally suggested by Hongo *et al.* (1968). Furthermore, it is in keeping with the latencies of the e.p.s.p.s classified as disynaptic from group II muscle afferent fibres.

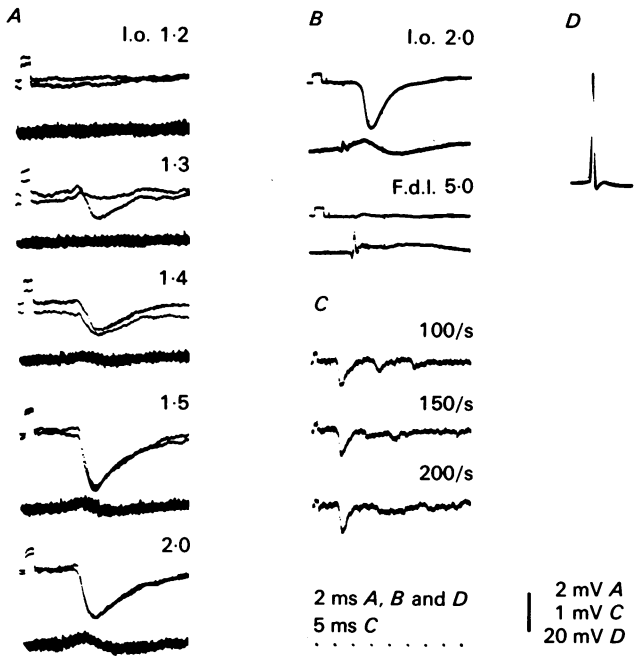

Fig. 2. The action of interosseous afferent fibres. *A*, graded stimulation of the interosseous nerve (I.o.) evoked i.p.s.p.s (upper traces) at low threshold. *B*, averaged i.p.s.p. on stimulating the interosseous nerve at twice threshold. For comparison the effect of stimulating the nerve to flexor digitorum longus (F.d.l.) is also shown. In *A* and *B* notice the negative cord dorsum potential which follows the interosseous group I volley at short latency (lower traces). *C*, stimulation of the interosseous nerve with three shocks at twice threshold and different frequencies reveals that the i.p.s.p.s have poor frequency-following capabilities. *D*, the antidromic spike of this s.c.t. neurone. The calibration pulses in *B* are 200 μV.

One further point of interest with regard to this inhibition is that it often failed to follow even moderately high frequencies. The i.p.s.p. in Fig. 2 barely followed even 100 stimuli/s and at 200 stimuli/s only the first of the repetitive stimuli evoked an i.p.s.p. (Fig. 2*C*). This is of interest in relation to studies involving high frequency activation of Pacinian corpuscles since, although high frequency activation may be a particularly effective stimulus for Pacinian corpuscles, the properties of the neuronal pathway are such that only the first volley of a high frequency train may be transmitted, at least in the pathway to s.c.t. neurones.

Actions evoked by the interosseous nerve at low strength were not exclusively inhibitory. Short latency excitation, which has not been reported previously, was

evoked in three neurones and Fig. 3 *B* shows an example. The threshold for this e.p.s.p. was 1·1 times nerve threshold and it will be noticed that it appeared with the same latency as the group II e.p.s.p.s; both most likely being evoked disynaptically. In addition, higher threshold, longer latency excitation was observed in three other neurones.

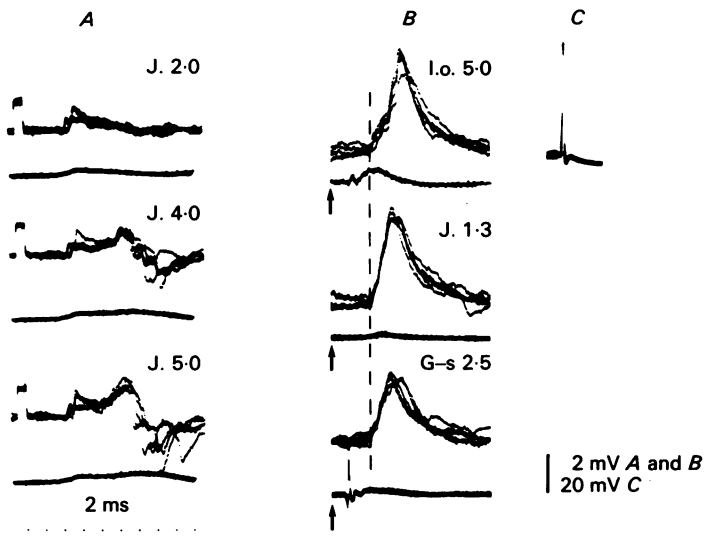

Fig. 3. The action of joint afferent fibres. *A*, records showing that graded stimulation of the joint nerve (J.) evoked short latency excitation at low threshold and long latency inhibition at higher threshold. In this example, the long latency inhibition was preceded by high threshold excitation which is most clearly seen at five times threshold. *B*, records from another s.c.t. neurone showing short latency excitation evoked from the joint nerve. For comparison of latencies, the effect of stimulating the interosseous nerve (I.o.) and group II afferent fibres of gastrocnemius–soleus (G–s) are also shown. The traces have been aligned to compare latencies from the application of the stimulus, which occurs at the beginning of each trace, as indicated by the arrows. Thus the e.p.s.p. evoked from the joint nerve is of comparable latency to e.p.s.p.s presumed to be disynaptic from the interosseous and gastrocnemius–soleus nerves. *C*, antidromic spike of the s.c.t. neurone shown in *B*.

Joint afferent fibres

Electrical stimulation of the posterior nerve to the knee joint regularly evoked excitation and/or inhibition. The excitation, which was evoked at low threshold (below twice threshold, in ten neurones) and short latency (4·0–6·3 ms from the stimulus), has not been previously reported. Our sample did not, on the other hand, include any s.c.t. neurones with early i.p.s.p.s which were occasionally seen by Hongo *et al.* (1968). The inhibition was always evoked at higher threshold (greater than four times threshold, in nine neurones) and longer latency (10–12 ms from the stimulus). Occasionally excitation was also evoked at an intermediate latency (in three neurones). These different post-synaptic responses were not always evoked in the same cells. In fact, it was more usual to observe either one or another type of response in different cells, although a combination of responses was also observed. The cell

illustrated in Fig. 3*A* was unusual in the respect that all three types of response were clearly observed. With increasing intensity the stimulus evoked first an excitation which reached a maximum at twice threshold. Stronger stimuli evoked the later inhibition, which was clearly seen at four times threshold and which was preceded by the generally less frequent late excitation. Both of these late potentials grew as the stimulus strength was increased further.

From the preceding sections we can conclude with reasonable certainty that the *minimal* synaptic linkage for interosseous and muscle afferent fibres is disynaptic, since these two nerves display a clear group I volley from which the central latencies can be measured (after allowing for an additional conduction time for more slowly conducting afferent fibres). On the other hand, the synaptic linkage of joint afferent fibres is more difficult to estimate, since the arrival of the afferent volley can often not be detected with certainty in the record from the dorsal root entry zone. However, measured from the stimulus the early excitation evoked from the joint nerve occurred with a range of latencies similar to that of the early p.s.p.s evoked from muscle and interosseous afferent fibres (4·0–6·3 ms compared to 3·5–7·0 ms and 3·5–5·0 ms, respectively). Furthermore, in individual neurones the latencies of the e.p.s.p.s evoked from the joint nerve were virtually the same as of those evoked from the interosseous and muscle nerves. Fig. 3*B* shows an example of such e.p.s.p.s. Thus with similar conduction distances and presumed conduction velocities of the effective joint afferent fibres, it is conceivable that the minimal synaptic linkage for joint afferent fibres is also disynaptic.

Effects from the pyramidal tract

Single stimuli applied to the pyramidal tract evoked a variable number of e.p.s.p.s, each e.p.s.p. being of constant latency and amplitude. These e.p.s.p.s were considered as unitary in view of their appearance in an all-or-nothing fashion as illustrated in Fig. 4. Records in Fig. 4*A* show that a 50 μA pyramidal stimulus evoked two large e.p.s.p.s and a number of smaller ones. Upon reducing the stimulus strength to 35 μA the earliest large e.p.s.p. disappeared and the other e.p.s.p.s remained unchanged. The later e.p.s.p.s of Fig. 4*B* likewise disappeared in a unitary manner upon reducing the stimulus strength. As many as seven such potentials could be distinguished clearly in records from a single neurone by moving the position of the stimulating electrode within the pyramid. Such properties suggested that each unitary potential was the result of the monosynaptic action from a single pyramidal tract fibre. This contention is supported by the fact that these e.p.s.p.s followed a frequency of 800 Hz (see below and Fig. 6). On the other hand it was difficult to measure the segmental latency of these e.p.s.p.s (in relation to the descending volleys responsible for them) since the pyramidal volleys are highly dispersed on reaching the lumbar levels of the cord (Lloyd, 1941; Lundberg & Voorhoeve, 1962). Fig. 5 shows the temporal dispersion of the pyramidal volley as it travels caudally. At C3 the volley was fairly well synchronized, but upon reaching Th13 and more caudal segments the volley was so dispersed that its duration exceeded the length of the trace. Nerve impulses in the fastest pyramidal fibres arrived at the L6/L7 border at about 4 ms latency, which clearly allowed the earliest unitary e.p.s.p.s to be evoked with a monosynaptic latency. However, the later e.p.s.p.s would also be fully compatible with the

monosynaptic action of more slowly conducting pyramidal tract fibres. Such unitary e.p.s.p.s were observed in eighteen neurones.

While we argue that the e.p.s.p.s shown in the histogram were due to the monosynaptic action of pyramidal tract fibres, we do not argue that the distribution of occurrence of these e.p.s.p.s is a fair reflexion of the occurrence of unitary e.p.s.p.s. On the contrary, our sample is biased towards the earliest e.p.s.p.s since the largest e.p.s.p.s tended to occur with the shortest latencies and we certainly missed any very small e.p.s.p.s or e.p.s.p.s which fell outside the duration of our averaging period.

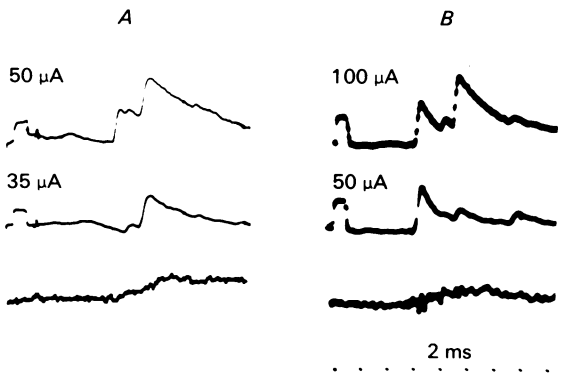

Fig. 4. Effects of single shock stimulation of the pyramid. *A*, 50 μA evoked a number of e.p.s.p.s of different latencies. Reduction of the stimulus strength to 35 μA no longer evoked the first large e.p.s.p. but the later ones remained unchanged. *B*, the same as *A* but in another s.c.t. neurone. A reduction of the stimulus strength from 100 μA to 50 μA failed to evoke the second large e.p.s.p. although the others remained unchanged. Lowermost traces, records from the cord dorsum. The calibration pulse at the beginning of each trace is 200 μV.

It is of additional interest that the largest e.p.s.p.s were usually among those with the shortest latency, since this suggests that the fastest conducting fibres (those with the largest diameter) evoke the largest unitary e.p.s.p.s. This phenomenon appears to be the rule for other monosynaptic e.p.s.p.s (see Mendell & Henneman, 1971; Lüscher, Ruenzel, Fetz & Henneman, 1979; Harrison & Taylor, 1981; Kirkwood & Sears, 1982) and it has been suggested to reflect the ability of an axon to branch, which will therefore determine the extent of the terminal arborizations and therefore the number of active terminals (Mendell & Henneman, 1971; Lüscher *et al.* 1979).

On some occasions the amplitudes of the unitary e.p.s.p.s increased upon repetitive stimulation. In Fig. 6*A* is shown an example of this with superimposed single sweep records and in Fig. 6*B* with averaging. It appeared that such facilitation was frequency-dependent, as shown in Fig. 6*C*. Thus, increasing the frequency of stimuli (shortening the interstimulus interval) increased the degree of facilitation, as has been reported for the monosynaptic action of corticospinal fibres on motoneurones in the monkey (Porter, 1970; Muir & Porter, 1973).

Actions evoked from the pyramids were not limited to monosynaptic e.p.s.p.s. Polysynaptic actions were frequent and were most clearly seen with repetitive and only rarely with single stimuli. Inhibition was then by far the most frequently

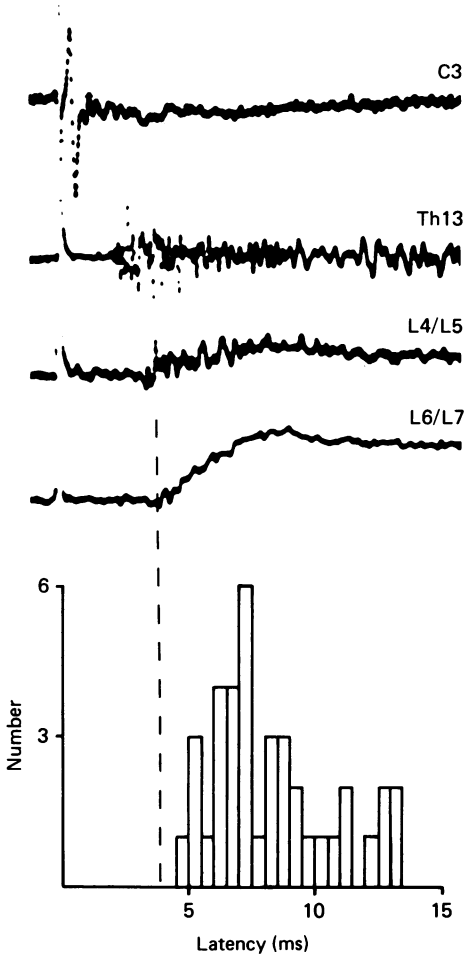

Fig. 5. Histogram showing latencies of e.p.s.p.s evoked from the pyramid. The upper four traces show averaged records from the cord dorsum at different segments in order to illustrate the temporal dispersion of the pyramidal volley as it travels caudally. Note that at the L6/L7 border the pyramidal activity is primarily represented by a negative cord dorsum potential, with little superimposed spike activity. The onset of the spike activity at the L6/L7 border precedes the earliest e.p.s.p.s with a latency compatible with monosynaptic connectivity.

observed effect. Some polysynaptic actions are illustrated in Fig. 7. Single stimuli evoked only monosynaptic unitary e.p.s.p.s whereas two stimuli were sufficient to facilitate the interposed interneurones and evoke later i.p.s.p.s (Fig. 7*A*) or both i.p.s.p.s and e.p.s.p.s (Fig. 7*B–D*).

The red nucleus

Although actions evoked from the red nucleus were searched for as routinely as from the pyramids, no clear p.s.p.s were usually evoked with single, double or triple stimuli of less than 100 μA, or even 200 μA. In other studies involving stimulation

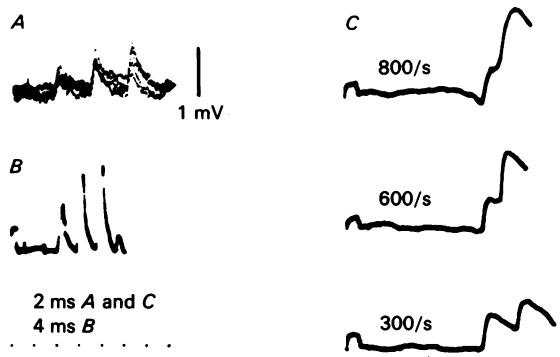

Fig. 6. Facilitation of unitary e.p.s.p.s with repetitive stimulation using 100 μA shocks to the pyramid with single sweeps (*A*) and with averaging (*B*). In another neurone (*C*) the facilitation increased with increasing frequency of the stimuli (40 μA). The calibration pulse at the beginning of each trace in *B* and *C* is 200 μV.

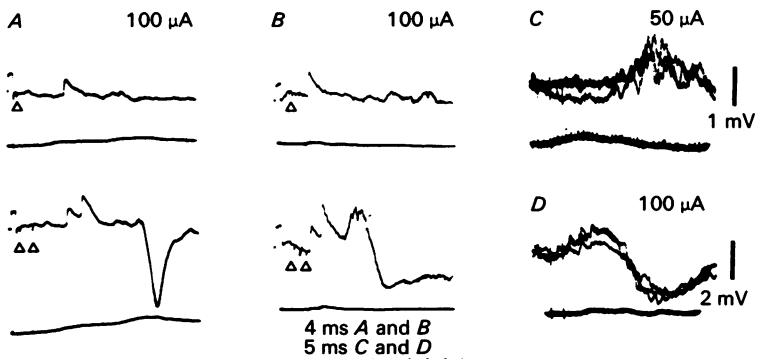

Fig. 7. Polysynaptic actions evoked from the pyramid revealed with double stimuli. In the two illustrated s.c.t. neurones (*A* and *B*) a single 100 μA shock to the pyramid evoked only a single unitary e.p.s.p. However, double stimuli evoked, in addition to the unitary e.p.s.p.s, longer latency polysynaptic inhibition (*A*) or excitation and inhibition (*B*). The calibration pulse at the beginning of each trace in *A* and *B* is 200 μV.

of the red nucleus, stimuli of less than 50 μA were sufficient to evoke discharges in rubrospinal tract neurones and to evoke p.s.p.s in their target neurones (e.g. Hongo *et al.* 1969; Baldissera *et al.* 1972). It is thus tentatively concluded that rubrospinal neurones either do not or only negligibly affect s.c.t. neurones.

It was however the case that stimuli of 100–200 μA occasionally evoked small e.p.s.p.s or i.p.s.p.s in s.c.t. neurones, especially when longer trains of stimuli were used. Since such stimuli may activate other neuronal systems in addition to rubrospinal neurones (Baldissera *et al.* 1972; cf. also Jeneskog & Johansson, 1977), these p.s.p.s can be attributed to such a neuronal system (or systems). This possibility is substantiated by records of Fig. 8, which shows p.s.p.s evoked in a cell for which a train of stimuli of 35 μA (six stimuli, 300 stimuli/s) was ineffective when applied within the red nucleus yet was effective when the electrode was withdrawn to a position 1 mm dorsal to the red nucleus.

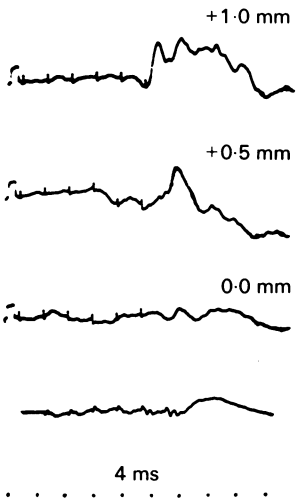

Fig. 8. The action of stimuli in and around the red nucleus. Repetitive stimuli (six shocks; 35 μA) applied in the red nucleus evoked no action in this neurone. However, raising the electrode dorsally evoked clear excitation at 1 mm above the red nucleus. The calibration pulse at the beginning of each trace is 200 μV.

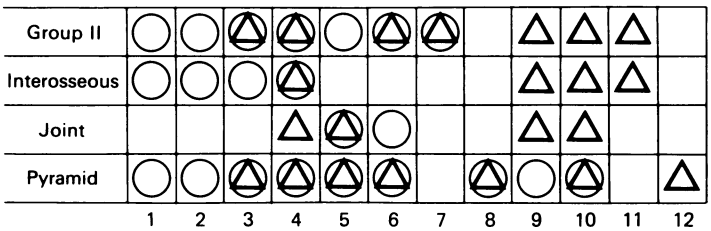

Fig. 9. Patterns of convergence exhibited by a sample of twelve s.c.t. neurones. All four sources of input were tested for each neurone. The data for each s.c.t. neurone are represented by a column. Circles represent excitation, triangles represent inhibition evoked by the different fibre systems. All neurones were excited by low threshold cutaneous afferent fibres.

Convergence on individual s.c.t. neurones

In addition to the monosynaptic excitation from cutaneous nerves, individual s.c.t. neurones were excited and/or inhibited from various other sources. Thus, of thirty-four s.c.t. neurones, eighteen were excited by corticospinal fibres, fourteen were excited by group II muscle afferent fibres, twelve were inhibited from interosseous afferent fibres, ten were excited by joint afferent fibres, etc. Since these figures are underestimates due to the fact that we did not test actions of all types of fibres in all neurones, the total number of e.p.s.p.s and i.p.s.p.s of different origin clearly exceeded the number of neurones in the sample. It follows that several types of fibre converged on to individual neurones, as is illustrated for a sample of twelve neurones in Fig. 9. The Figure also shows that the *patterns* of convergence varied from one neurone to the next.

DISCUSSION

Intracellular recording used in the present study has been particularly useful for revealing various actions not readily seen with extracellular recording and for defining the pathways involved. For example, it appeared previously as if afferent fibres of Pacinian corpuscles did not influence s.c.t. neurones (see Brown, 1981*b*). However, by combining intracellular recording with electrical stimulation of the interosseous nerve, and by taking advantage of the rich supply of afferent fibres of Pacinian corpuscles in this nerve (Hunt & McIntyre, 1960), it has been demonstrated that Pacinian afferent fibres may both excite and inhibit s.c.t. neurones. With respect to group II afferent fibres, Hamman *et al.* (1978) found excitatory actions upon discharges of less than 10% of s.c.t. neurones, without evidence for any inhibitory actions, while in the present experiments intracellular recording revealed i.p.s.p.s as well as e.p.s.p.s in a substantial proportion of s.c.t. neurones. Previously undisclosed excitatory post-synaptic actions have been found from lowest threshold joint afferent fibres in addition to the post-synaptic inhibition described by Hongo *et al.* (1968). The facilitatory and inhibitory actions from corticospinal tract fibres which were previously explained by presynaptic actions of these fibres (see below) have also been shown to include a post-synaptic component.

It is of interest to note that, in general, such non-cutaneous sources of input only rarely evoked discharges in s.c.t. neurones, and the significance of such subthreshold actions is not as apparent as that of the strongest input from cutaneous afferent fibres, which has been extensively discussed in the literature. We therefore deliberately wanted to draw attention to the weaker synaptic actions of non-cutaneous origin with the hope of provoking thought into designing experiments to assess the functional meaning of these actions.

The shortest latency post-synaptic actions of non-cutaneous afferent fibres reported here appear to be evoked through disynaptic pathways. A disynaptic (rather than polysynaptic) coupling in these pathways simplifies the problem of defining the neuronal systems involved in the afferent control of s.c.t. neurones and ultimately in explaining its functional meaning. One possibility to consider is that the disynaptic e.p.s.p.s reflect a linkage between s.c.t. neurones and neurones with axons ascending the dorsal columns (d.c. neurones). Strong indications have been found for collateral excitation of d.c. neurones by s.c.t. neurones (Jankowska, Rastad & Zarzecki, 1979). On the other hand, collateral excitation of s.c.t. neurones by d.c. neurones has been considered unlikely (Brown, 1981*b*). The reason for this was that the type of input to d.c. neurones appeared not to be matched by similar input to s.c.t. neurones (Brown & Fyffe, 1981). However, the results of the present study alleviate this objection. Short latency excitation of d.c. neurones from group II and joint afferent fibres (Jankowska *et al.* 1979) and the effective actions from Pacinian corpuscles (Brown & Fyffe, 1981) would clearly allow d.c. neurones to mediate the post-synaptic actions found in this study; especially if it turns out that excitation of d.c. neurones from Pacinian afferent fibres is evoked at a mono- or disynaptic latency. The same d.c. neurones might likewise mediate oligo- or polysynaptic e.p.s.p.s of pyramidal origin because d.c. neurones themselves are excited by corticospinal fibres at a short latency (Jankowska *et al.* 1979).

With respect to the descending control of s.c.t. neurones it is well established that transmission through these neurones is under such control, but both the mechanisms of the descending control and the origins of the pathways involved are largely unknown (see Brown, 1981*a*, *b*). Previous investigations have been made by comparing the responsiveness of s.c.t. neurones before and after procedures such as cold block of the spinal cord (Brown, 1971; Cervero *et al.* 1977; Hong, Kniffki, Mense, Schmidt & Wendisch, 1979), removal of the cerebellum, transection of the brain stem, cutting and stimulating the dorsal columns (Brown & Martin, 1973) or intraspinal stimulation (Brown, Kirk & Martin, 1973). These studies were not selective for any particular descending fibre system. In addition, approaches using intraspinal stimulation and stimulation of the dorsal columns have been complicated by the possibility that such stimuli will also antidromically activate ascending neurones, and since some of these neurones give off collaterals at various spinal levels, any actions observed may well have been evoked either directly or indirectly by such collaterals. These previous studies have suggested that the descending control of activity of s.c.t. neurones operates primarily by gating the input to these neurones or, in other words, that descending actions are not so much upon s.c.t. neurones themselves as on neurones interposed in pathways to s.c.t. neurones or on primary afferents (see Brown, 1981*a*). This conclusion was based primarily on two kinds of observation. First, monosynaptic excitation of s.c.t. neurones appeared to be either unaffected, or much less affected than the polysynaptic excitation or inhibition of peripheral origin (Brown *et al.* 1973; Brown & Martin, 1973; Brown, 1981*a*). The second kind of observation relates to the time course of the descending inhibition, which has been found to be similar to the time course of presynaptic inhibition or primary afferent depolarization (Brown *et al.* 1973; Brown & Martin, 1973; Brown & Short, 1974). Brown & Short (1974) have, in fact, related the primary afferent depolarization not only to the descending inhibition but also to the descending facilitation of cortical origin (see also Lundberg, Norrsell & Voorhoeve, 1963). The facilitation was considered as most probably due to the activation of cutaneous afferent fibres, as in the cases of dorsal root reflexes; it was proposed that it was evoked by intense depolarization produced in them by cortical stimulation (Andersen, Eccles & Sears, 1962; Carpenter, Lundberg & Norrsell, 1962).

Whatever the contribution of the presynaptic mechanisms to the descending control of s.c.t. neurones, the results of the present study demonstrate clear post-synaptic excitatory and inhibitory actions on stimulation of medullary pyramids. Of these post-synaptic actions the inhibition often outweighed the excitation, as in the effects of cortical stimulation upon discharges of s.c.t. neurones.

Of the post-synaptic actions following pyramidal stimulation, the excitation is especially worth noting, not only because excitatory descending influences upon s.c.t. neurones have been observed only rarely but also because the excitation is to a great extent evoked monosynaptically. The corticospinal control of s.c.t. neurones further emphasizes the role of some corticospinal neurones in the transfer of information via lemniscal pathways. Thus, since d.c. neurones and neurones of the dorsal column nuclei are also controlled by the cortex (Jankowska *et al.* 1979; Cole & Gordon, 1983), it is becoming increasingly apparent that the cortex generally has control over second order relay neurones in lemniscal pathways. In this context it should be pointed out

that the occurrence of monosynaptic excitation of s.c.t. neurones is in accordance with the anatomical observations that corticospinal neurones taking origin in the *somatosensory* cortex terminate mainly in laminae IV and V of the lumbosacral cord (Nyberg-Hansén & Brodal, 1963), an area of the cord clearly co-extensive with the location of both s.c.t. and d.c. neurones.

Brown (1971) has categorized s.c.t. neurones into four distinct types, depending on the combination of input from different cutaneous receptors. Electrical stimulation of cutaneous nerves did not allow us to recognize neurones of these four types in our sample, nor did responses of individual neurones to various stimuli indicate any clear-cut groups related to Brown's subdivision of s.c.t. neurones. While in all neurones monosynaptic e.p.s.p.s were evoked by low threshold cutaneous afferent fibres, of the other sources of input tested each influenced only a proportion of the sample. Furthermore, each of these other sources of input influenced a different proportion, so that the number of combinations of input was too large to allow any simple classification of the neurones into a few distinct groups.

The large degree of convergence from different peripheral and descending systems on to individual neurones is of special functional interest, since it indicates that individual s.c.t. neurones operate not as simple relay neurones but rather integrate information from a variety of different sources before forwarding it to supraspinal structures. Thus, while s.c.t. neurones respond to large diameter cutaneous afferent fibres in a highly faithful manner, the efficacy of transmission through these neurones is clearly modulated by a variety of both peripheral and descending sources.

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