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Ascending tract neurones processing information from group II muscle afferents in sacral segments of the feline spinal cord

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1. Ascending tract neurones located in the dorsal horn of sacral segments of the spinal cord have been investigated by extracellular and intracellular recording in the anaesthetized cat. The aim was to determine whether information from group II afferents that terminate within the sacral segments is conveyed to supraspinal structures and which types of neurones are involved.
2. A considerable proportion of ascending tract neurones found in the dorsal horn in the same segments as the pudendal (Onuf's) motor nucleus were excited by group II muscle afferents. The great majority (93 %) of these neurones had axons ascending in ipsilateral funiculi. Spinocervical tract neurones constituted the largest proportion (82 %) of such neurones, while very few spinocerebellar tract and propriospinal neurones and no post-synaptic dorsal column neurones were found among them.
3. In addition to activation by group II muscle afferents all of the neurones were strongly excited by cutaneous afferents. The most potent excitation was evoked by afferents of the posterior biceps–semitendinosus and gastrocnemius muscle nerves and by afferents of the cutaneous femoris, sural and pudendal nerves. The latencies of intracellularly recorded excitatory potentials were indicative of a high incidence of monosynaptic coupling between the afferents and ascending tract neurones.
4. The highly effective monosynaptic excitation of spinocervical tract neurones in the sacral segments by group II afferents is in contrast to the weak disynaptically mediated actions of group II afferents on such neurones in the L6–L7 segments but comparable to the actions of group II afferents on ascending tract neurones in the midlumbar segments.
5. Both the patterns of peripheral input and the latencies of synaptic actions in ascending tract neurones were similar to those in interneurones at the same locations (accompanying report). Similar information is therefore likely to be processed by both categories of neurones.
6. The role of sacral spinocervical tract neurones as a system for transmitting information from group II muscle afferents to supraspinal centres and the potential contribution of this system to the perception of limb position are discussed.

In addition to its contribution to the reflex control of movement, information from muscle, joint and skin receptors is required for the awareness of the movement and position of joints. With respect to information from group II spindle afferents, it has been recognized that a signal related to muscle length is especially useful for position sense (for reviews see Burgess, Wei, Clarke & Simon, 1982; Matthews, 1982). However, there is little firm evidence that group II muscle afferents contribute to kinesthesia and even the extent to which information from these afferents is forwarded to higher centres in the brain remains to be clarified.

Group II afferents from muscles of the cat hindlimb ascend in the dorsal columns no further than the thoracic segments (Lloyd & McIntyre, 1950; Fern, Harrison & Riddell, 1988) so that any information from these afferents which reaches supraspinal centres must be conveyed by second-order neurones. One of the main regions of termination of group II afferents of hindlimb muscles is in the midlumbar segments (Edgley & Jankowska, 1987*a*, *b*). Dorsal horn spinocerebellar tract neurones in these segments forward information from group II afferents to the cerebellum (Edgley & Jankowska, 1988; Edgley & Gallimore, 1988) and also, by axon collaterals of some of these neurones, to the region of nucleus Z (Asif & Edgley, 1992). However, the group II input to these neurones is provided by afferents of only a few hindlimb muscles, primarily those of the quadriceps, sartorius and pretibial

flexors. In a recent study we have found that another important relay for group II muscle afferents exists in the dorsal horn of sacral segments (Jankowska & Riddell, 1993). As reported in the companion paper (Jankowska & Riddell, 1994), interneurones in this region process information provided primarily by group II afferents of the posterior biceps–semitendinosus and triceps surae muscle nerves. The aim of the present experiments was to find out whether information processed in the sacral group II relay region is transmitted to supraspinal levels and whether the neurones responsible form part of the spinocerebellar or other ascending pathways.

METHODS

Preparation

The experiments were performed on eight cats, four of which were also used for experiments described in the companion paper (Jankowska & Riddell, 1994), in which the details of the preparation, the animal care and the main experimental procedures are described in greater detail. The cats were deeply anaesthetized, anaesthesia being induced with a single dose of pentobarbitone sodium (40 mg kg^{-1} I.P.) and maintained with several doses of chloralose (up to 50 mg kg^{-1} I.V.). The adequacy of anaesthesia was assessed by monitoring withdrawal reflexes and the corneal and pupillary reflexes during the surgery and by monitoring the blood pressure and diameter of the pupils during the experiments when the animals were paralysed with gallamine triethiodide and artificially ventilated.

A number of left hindlimb peripheral nerves were dissected free and mounted on electrodes. These routinely included: quadriceps (Q), sartorius (Sart), posterior biceps and semitendinosus (PBST), anterior biceps and semimembranosus (ABSM), medial gastrocnemius, lateral gastrocnemius and soleus (GS), plantaris (Pl), deep peroneal (DP, i.e. tibialis anterior and extensor digitorum longus from which the mixed nerve branch to the extensor digitorum brevis was removed), the caudal branch of sural (Sur) and the superficial peroneal (SP) nerves. Additional nerves dissected in some experiments included: gracilis (Grac), flexor digitorum longus (FDL, dissected free from the interosseous nerve), the remaining part of the tibial (Tib), saphenous (Saph), pudendal (Pud), and the cutaneous femoris (CF) nerves. The spinal cord was exposed from the fourth lumbar to the sacral segments and at the level of the 13th thoracic (Th13) segment. In three cats a laminectomy was also made at an upper cervical level and in two cats a craniotomy was made over the middle of the cerebellum.

Recording and stimulation procedures

Neurones were selected for investigation on the basis of short latency synaptic responses to stimuli activating cutaneous and/or group II muscle afferents and antidromic responses following stimuli applied to the lateral funiculi rostral to the lumbosacral enlargement (Th13). Such neurones were searched for within a roughly 5 mm long section of the spinal cord containing and extending rostral to Onuf's nucleus, dorsal to which group II afferents, in particular those of PBST, have strong synaptic actions (Jankowska & Riddell, 1993, 1994). The largest cord dorsum potentials evoked by group II afferents of the PBST nerve and by afferents of the pudendal nerve were used to locate this region (see Jankowska & Riddell, 1993) and neurones were searched for over a range of depths where field potentials evoked by these afferents were largest (usually 1·0–1·5 mm from the surface). A recording electrode was left in each of the areas explored for subsequent histological identification of recording sites that were related to the rostral border of Onuf's nucleus (for further details see Jankowska & Riddell, 1993). Recording from neurones was carried out using glass microelectrodes filled with 2 M potassium citrate solution (1–1·5 μm tip diameter, 3–5 MΩ resistance). Recordings from neurones were usually first made extracellularly and tested to determine how far rostrally and on which side of the spinal cord they projected.

To determine whether neurones projected beyond the lumbosacral enlargement they were first tested for their response to stimulation of the ipsilateral and contralateral lateral funiculus at Th13. Neurones failing to be antidromically activated were considered interneurones and their properties are described in the companion paper (Jankowska & Riddell, 1994). In three experiments stimuli were applied to the lateral funiculus of cervical segments to determine whether the axons of the tested neurones terminated within the spinal cord or projected beyond it. The lateral funiculi at the Th12–13 and C1–3 levels were stimulated transdurally with 0·2 ms current pulses. Cells antidromically activated by stimuli applied to the lateral funiculus at C3 but not activated, or responding only at significantly higher stimulus strengths at C1 were considered to terminate within the lateral cervical nucleus and to be spinocervical tract (SCT) neurones (see Brown, 1981). When no response occurred at lower strengths, stimuli were increased to at least 500 μA and often 1 mA. Judging from the large negative cord dorsum potentials evoked at the sacral level, such stimuli activated many axons in the dorsal columns and might have activated postsynaptic dorsal column neurones. To ensure a more reliable activation of such cells in one cat the dorsal columns were dissected over a 2 cm distance at the Th12–13 level and stimulated directly while searching for ascending tract cells.

In two experiments tungsten electrodes with exposed tips of some 100 μm were inserted into the anterior lobe of the cerebellum to determine whether any sacral ascending tract neurones could be antidromically activated by stimuli applied within the cerebellum. The electrodes were first positioned (following the procedure of Edgley & Gallimore, 1988) at locations from which Clarke's column cells were activated by stimuli of less than 50 μA (0·2 ms rectangular pulses). Clarke's column cells were identified as cells located in the most medial part of the dorsal horn at the border between the L3 and L4 segments, antidromically activated by stimuli applied to the ipsilateral lateral funiculus at a cervical level and/or the cerebellum and monosynaptically excited by group I afferents of one of the muscle nerves. Their location was subsequently verified histologically. Search stimuli of 200–500 μA were then applied in the same and nearby regions of the cerebellum, especially at locations 1–2 mm deeper, since spinocerebellar neurones from more caudal spinal segments (L7–S3 as compared to L2–L7) are reported to terminate to a greater extent within the deeper cerebellar lobuli (I and II rather than III–IV; Matsushita, 1988). The electrodes were inserted at the level of the fissura prima, 2–3 mm from the mid-line. They were advanced at an angle of 30–45 deg (with the tip directed rostrally), to a depth of 9–12 mm from the surface in order to reach an area just rostral to the left nucleus interpositus (at a

horizontal level of about H0). Small electrolytic lesions were made at the end of the experiments to mark the stimulation sites, which were subsequently histologically identified.

All antidromic responses were confirmed by collision of orthodromically conducted impulses evoked from peripheral nerves with presumed antidromic impulses.

Following tests of projection an attempt was made to penetrate the neurone, either in the same electrode track or in tracks 20–100 μm away. After successful penetrations antidromic responses were confirmed and PSPs evoked from peripheral nerves were recorded intracellularly. Peripheral nerves were stimulated with 0·1 ms rectangular current pulses (single or double stimuli, 2·5 or 3·3 ms apart). Stimulus strengths are expressed relative to threshold (T) for the most excitable afferents in the nerve. A silver ball electrode placed about 5 mm rostral of the microelectrode was used for recording afferent volleys from the surface of the spinal cord. The records were photographed directly from the oscilloscope screen and stored on a tape-recorder. When the recording was stable over a sufficiently long period of time, the records were also averaged (on or off line) using a Nicolet Instrument Corporation (Madison, WI, USA) averager (type 1170, 5 μs per address, averages of 16–64 individual potentials).

RESULTS

Types of ascending tract neurones in the sacral dorsal horn

All of the sample of seventy-three neurones investigated in this study responded at short latency (< 4 ms) to electrical stimulation of cutaneous and/or group II muscle afferents and projected rostral to the lumbosacral enlargement as determined by an antidromically evoked response to stimuli applied at the Th13 level. Of these neurones, sixty-eight (93 %), projected within the ipsilateral lateral funiculus and five (7 %) in the contralateral lateral funiculus. Neurones with axons in the dorsal columns (Uddenberg, 1968; Angaut-Petit, 1975) were not encountered. No neurones were antidromically activated by stimulation of the dissected dorsal columns in one of the experiments. Furthermore, no neurones were antidromically activated when the intensity of stimulation of the lateral funiculus at the thoracic level was raised to 1 mA; this is well above the intensity required (less than 350 μA) to activate SCT

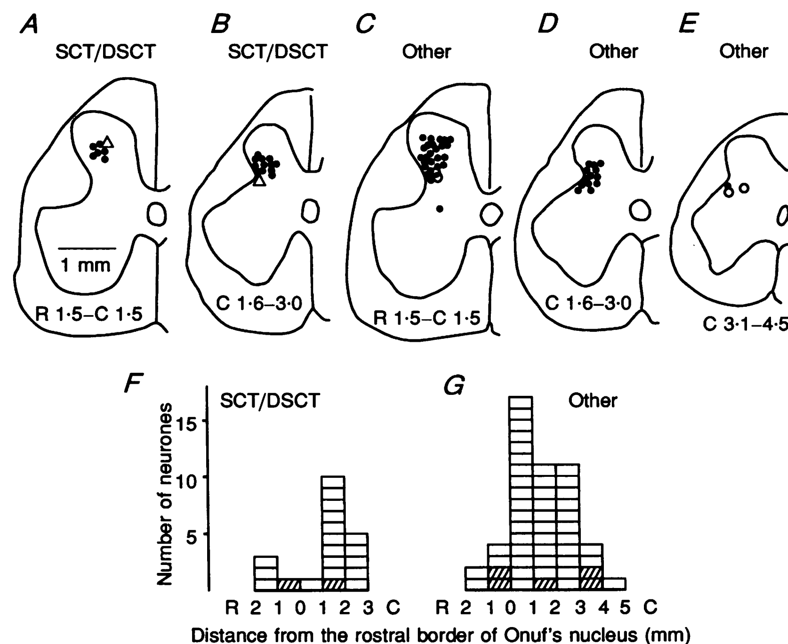

Figure 1. Location of the sample of neurones investigated in the present study

In A–E the location of neurones is plotted on representative outlines of the spinal cord in the transverse plane. The neurones have been divided into three groups according to their rostrocaudal location in relation to the histologically defined rostral border of Onuf's nucleus; 1·5 mm rostral–1·5 mm caudal (A and C), 1·6–3·0 mm caudal (B and D), and 3·1–4·5 mm caudal (E). The positions of the neurones were reconstructed from the depth of the recording electrode tip and the trajectory of the recording electrode in relation to the histologically defined position of a marking electrode. A and B, location of eighteen spinocervical (●) and two spinocerebellar (△) tract neurones. C–E, location of other unidentified ipsilaterally (●) and contralaterally (○) ascending neurones. F and G, rostrocaudal location of recorded neurones with respect to the rostral border of Onuf's nucleus (R, rostral; C, caudal). F shows data for spinocervical (□) and spinocerebellar (▨) tract neurones. G shows data for unidentified ipsilaterally (□) and contralaterally (▨) ascending neurones. SCT, spinocervical tract; DSCT, dorsal spinocerebellar tract.

neurones and, judging from the large negative cord dorsum potential that such stimuli evoked, resulted in the activation of many axons in the dorsal columns. *Neurones with axons within the ipsilateral lateral funiculus* therefore constitute the main type of neurones projecting beyond the lumbosacral enlargement from the sacral group II relay region.

The great majority of ipsilaterally ascending neurones projected to at least the C3 segment (26/31; 84 %) and might have terminated within the upper cervical segments or projected to supraspinal structures. Only five neurones (16 %) could not be antidromically activated from the C3 segment and were considered to be long-axoned propriospinal neurones.

Eighteen of twenty-two ipsilaterally projecting neurones (82 %) were identified as spinocervical tract (SCT) neurones, since they were activated by stimuli applied to the ipsilateral lateral funiculus at C3 (at a stimulus intensity of 70–250 μA) but not at C1, with the exception of a few neurones which responded to stimulation at intensities of 500–1000 μA. In the latter case activation is attributed either to stimulation of a thinner ascending axon collateral within the C1 segment (see Brown, 1981) or to spread of current to the C3 level. Records illustrating the procedure used to identify SCT neurones are shown in Fig. 2*C–E*.

Two out of eighteen ipsilaterally projecting neurones (11 %) which were tested for responses to stimuli applied within the cerebellum (see below) were identified as spinocerebellar tract neurones.

Given the large proportion of SCT neurones identified among the ascending tract neurones in the sacral dorsal horn, the majority of the twenty-three unidentified neurones (tested only by applying stimuli at the Th13 level) were most likely also to be SCT neurones. The properties of SCT and other ascending neurones are nevertheless presented separately.

Location of neurones

As shown in Fig. 1, all but one of the neurones studied were located within the lateral two-thirds of the dorsal horn. Rostrocaudally they were distributed within a length of the spinal cord containing, and extending about 1·5 mm rostral to, the pudendal (Onuf's) motor nucleus. They were therefore distributed within an area in which strong synaptic actions have been shown to be produced by group II muscle afferents (Jankowska & Riddell, 1993) and in which the interneurones described in the companion paper were located (Jankowska & Riddell, 1994).

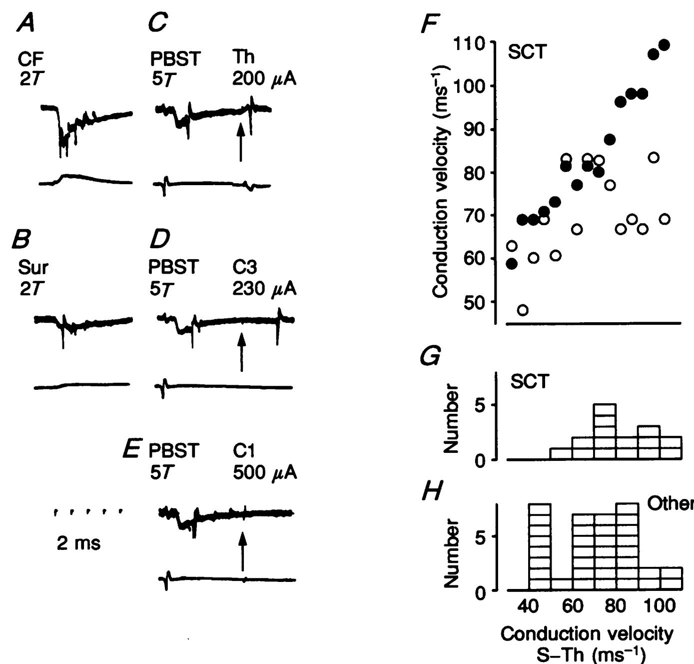

Figure 2. Examples of extracellular records from a SCT neurone and distribution of conduction velocities in the samples of SCT and unidentified sacral ascending tract cells

The top records in *A–E* show responses evoked by stimulation of cutaneous and group II muscle afferents; afferent volleys are shown in the lower records. The records in *C–E* show, in addition, the antidromically evoked responses upon stimulation of the lateral funiculus at the Th13 and C3 levels and the lack of response to much stronger stimuli at C1 (arrows indicate shock artifacts). The latter stimuli failed to activate the cell whether they were or were not preceded by the peripheral nerve stimulation. *F*, conduction velocities between the sacral and thoracic segments (S–Th, ●) and between the thoracic and cervical segments (Th–C, ○) for 15 of the 18 SCT neurones. *G* and *H*, histograms of conduction velocities, measured between the sacral and thoracic segments, of SCT (*G*) and other unidentified ipsilaterally ascending tract cells (*H*; excluding the 5 propriospinal neurones).

Properties of spinocervical tract (SCT) neurones

All eighteen of the neurones identified as SCT neurones were first detected and characterized during extracellular recordings. Subsequent intracellular recordings stable enough to enable a check of antidromic identification criteria and a full investigation of the excitatory and inhibitory actions of a range of peripheral afferents were made from seven neurones.

Axonal conduction velocities were calculated from the latencies of antidromic activation from the C3 segment (distances of 270–290 mm) and from the Th13 segment (distances of 85–90 mm) after having subtracted 0·2 ms for the latent period of activation of the axons by electrical stimuli. Overall conduction velocities (measured between the sacral and cervical segments) ranged from 53 to 89 m s^{-1}, most being of between 70 and 85 m s^{-1}. These neurones therefore represent the faster conducting fraction of lumbosacral SCT cells (see Brown, 1981, for references). For two-thirds of these neurones there was a slowing in the conduction velocity of between 10 and 40 m s^{-1} above the Th13 level. This tendency is illustrated in Fig. 2*F* where data for conduction velocities measured between the sacral recording site and Th13 are compared to those between Th13 and C3. This slowing, which has not been reported before, might be due to collateral branches arising from the axons of lumbosacral SCT neurones, perhaps within the cervical enlargement. The remaining one-third of the SCT neurones appeared to conduct with a similar conduction velocity throughout the length of their projection along the spinal cord.

Cutaneous excitatory input

Input from cutaneous afferents is a major feature of the SCT system and, as expected, cutaneous afferents provided the main peripheral input to sacral SCT neurones, seventeen of the eighteen extracellularly recorded neurones being activated by cutaneous afferents. The most potent source of excitation was the CF nerve, stimulation of which evoked a repetitive discharge (see example in Fig. 2*A*) of thirteen of the eighteen neurones tested. Cutaneous afferents of the sural nerve were also effective in nine of the eighteen SCT neurones, though they usually induced only

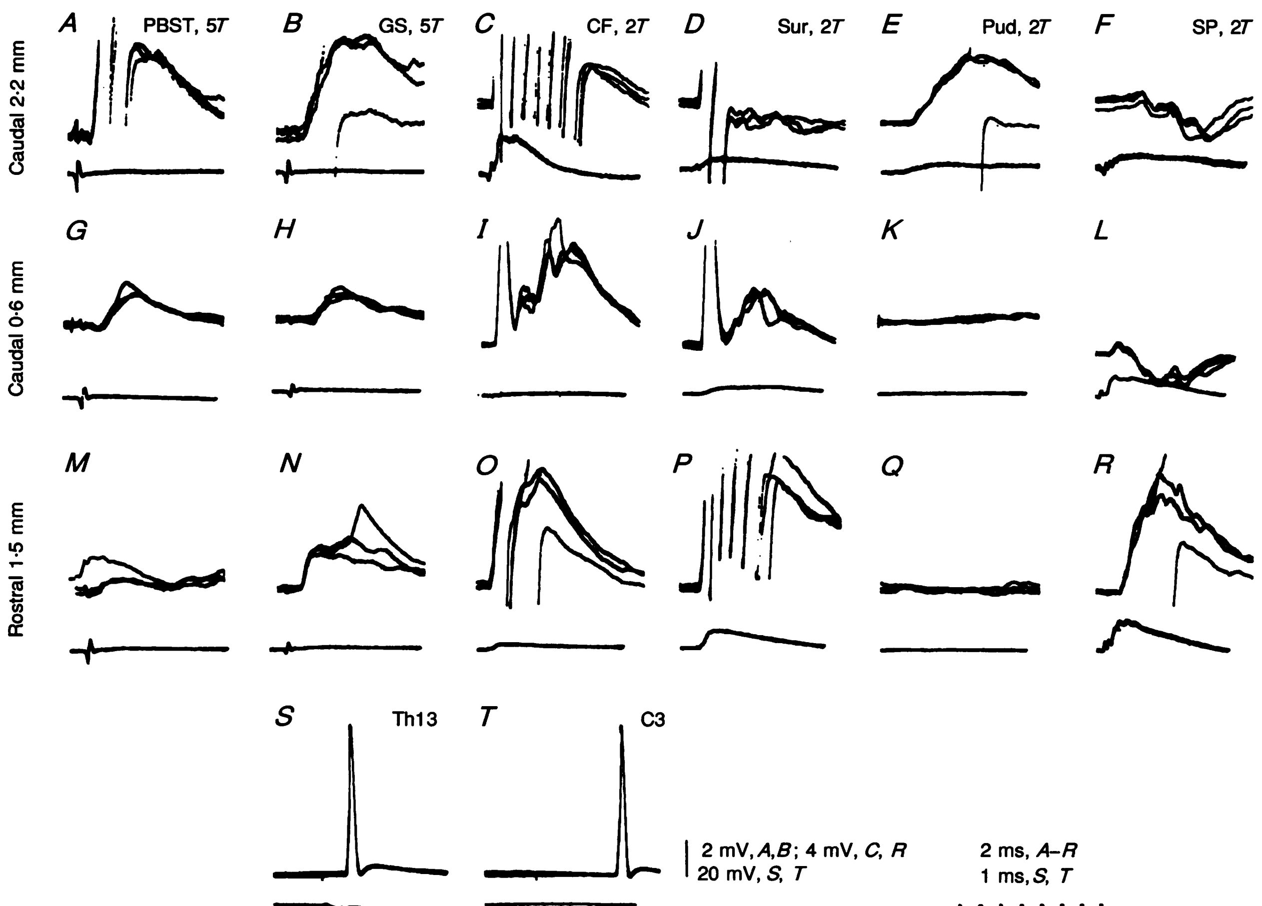

Figure 3. Examples of PSPs evoked in three SCT neurones from the same cat
The cells were located 2·2 and 0·6 mm caudal (*A–F* and *G–L*) and 1·5 mm rostral (*M–T*) to the rostral border of Onuf's nucleus. Upper traces are intracellular records. Lower traces are records from the surface of the spinal cord. The nerves stimulated and the stimulus intensities are indicated above the records. *S* and *T*, antidromic activation from the Th13 and C3 levels for the most rostral neurone.

a single or double discharge. Afferents of the SP and Pud nerves were rarely effective (discharging only 2 and 3 neurones respectively).

In addition to afferents from cutaneous receptors in skin around the genitalia and the perineal area the pudendal nerve contains afferents from mechanoreceptors associated with the urethra and rectum (Martin, Fletcher & Bradley, 1974). However, the latter are mainly slower conducting and likely to be of higher electrical threshold than the cutaneous afferents, so that the actions evoked from the pudendal nerve on the neurones of the present sample are considered most likely to be of cutaneous origin.

Of the seven SCT neurones from which records were subsequently made intracellularly, all displayed EPSPs evoked by afferents of CF (Fig. 3*C*, *I* and *O*) and all but one EPSP evoked by afferents of Sur (Fig. 3*D*, *J* and *P*). EPSPs evoked by afferents of Pud and SP were seen in fewer neurones and were generally smaller than those evoked by other cutaneous afferents (cf. the last two columns with the third and fourth columns of Fig. 3). EPSPs evoked from these nerves differed also with respect to their latencies. EPSPs evoked by afferents of CF and Sur were with only one exception of short, most probably monosynaptic, latencies while those of SP and Pud were almost all evoked at latencies compatible with a di- or trisynaptic coupling (see Fig. 5*D* and *E*).

There were also indications that the excitatory input from cutaneous afferents to SCT neurones differed depending on their rostrocaudal location. There was a tendency for excitation from Pud to occur only in the most caudal neurones (Fig. 3*E*, *K* and *Q*) and from SP only in the most rostral neurones (Fig. 3*F*, *L* and *R*). Similarly, there was a tendency for responses from CF to be stronger in the more caudally recorded neurones (Fig. 3 *C*, *I* and *O*) and for responses from Sur to be stronger in the more rostral neurones (Fig. 3*D*, *J* and *P*). These observations correlate with differences in the amplitudes of field potentials and in the input to interneurones at different rostrocaudal levels within this region of the sacral spinal cord (Jankowska & Riddell, 1993, 1994).

Muscle group II excitatory input

Stimuli near maximal for group II muscle afferents, i.e. 4–5*T*, induced discharges of more than two-thirds (13/18) of extracellularly recorded neurones and EPSPs in all seven intracellularly recorded neurones, none of the neurones being excited by stimuli subthreshold for group II afferents. The discharges evoked by group II muscle afferents were evoked with as high a security as by cutaneous afferents but consisted of only single action potentials (see Fig. 2*C*–*E*) while stimuli applied to cutaneous nerves induced either single or repetitive discharges.

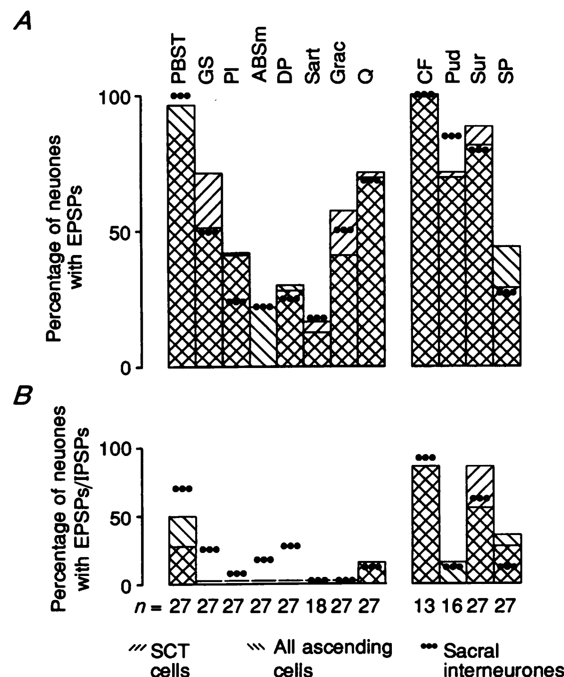

Figure 4. Proportions of intracellularly recorded sacral dorsal horn neurones with input from group II afferents of eight muscle nerves and low threshold afferents of four cutaneous nerves
A, proportions of neurones in which EPSPs were induced by stimulation of muscle nerves at 5*T* and cutaneous nerves at 2*T*. *B*, proportions of neurones in which EPSPs were followed by IPSPs. Different symbols (see key) are used to represent data for SCT neurones ($n = 7$, all nerves), the pooled population of all intracellularly recorded ascending tract neurones (including the SCT neurones; n as indicated) and a population of interneurones recorded from intracellularly in the same region (from Jankowska & Riddell, 1994). Note the similarity in the distribution of input to these three populations of neurones.

The most effective group II afferents, that is those which most frequently discharged extracellularly recorded neurones, were those of PBST (11/18), GS (7/18) and Q (4/18). The histograms of Fig. 4. show the proportions of SCT neurones in which group II muscle afferents of different nerves induced intracellularly recordable EPSPs. As with extracellularly recorded discharges, EPSPs were most frequently evoked by group II afferents of the PBST, GS and Q nerves. PBST afferents usually also evoked the largest EPSPs, as illustrated in Fig. 3*A* and *G*. However, as indicated in Fig. 4, EPSPs were also occasionally evoked by group II afferents of nerves which lacked appreciable extracellularly recordable effects (Pl, DP, Grac and Sart).

The plots in Fig. 5*A* and *B* show the latencies of intracellularly recorded EPSPs evoked by group II muscle afferents in identified SCT neurones (▩; together with data for other unidentified sacral ascending tract neurones, □). More than half of the EPSPs evoked by group II afferents of the PBST, GS and Q nerves occurred at latencies compatible with a monosynaptic coupling (for the ranges of latencies considered monosynaptic see legends to Fig. 5 and for the reasoning behind their derivation see Jankowska & Riddell, 1994). For comparison, Fig. 5*C* shows the latencies of EPSPs evoked by group II afferents of the PBST and GS nerves in a sample of lower lumbar (L6–L7) SCT neurones (Harrison & Jankowska, 1984) none of which occurred at latencies compatible with a monosynaptic connection.

As for the excitatory input from cutaneous afferents, there were indications that the excitatory actions of group II afferents of different muscle nerves varied according to the rostrocaudal location at which neurones were recorded. As illustrated in Fig. 3, in more caudally located neurones group II afferents in the PBST nerve tended to evoke larger and faster rising EPSPs than those of GS whilst in more rostral neurones this pattern was reversed.

Inhibitory input

Postsynaptic inhibition of SCT neurones in the lower lumbar segments has previously been shown to be evoked by natural stimulation of cutaneous receptors (Hongo, Jankowska & Lundberg, 1968; Brown, Koerber & Noble, 1987) and by electrical stimulation of cutaneous and group II muscle afferents (Harrison & Jankowska, 1984). In the sample of sacral SCT neurones investigated in this study, IPSPs were most effectively evoked by the same afferents as those that produced the strongest excitation. Since IPSPs were therefore normally preceded and often masked by EPSPs, enhancement of the IPSPs by depolarization of the cell membrane was usually required to disclose them. This is illustrated in Fig. 6, where IPSPs which followed

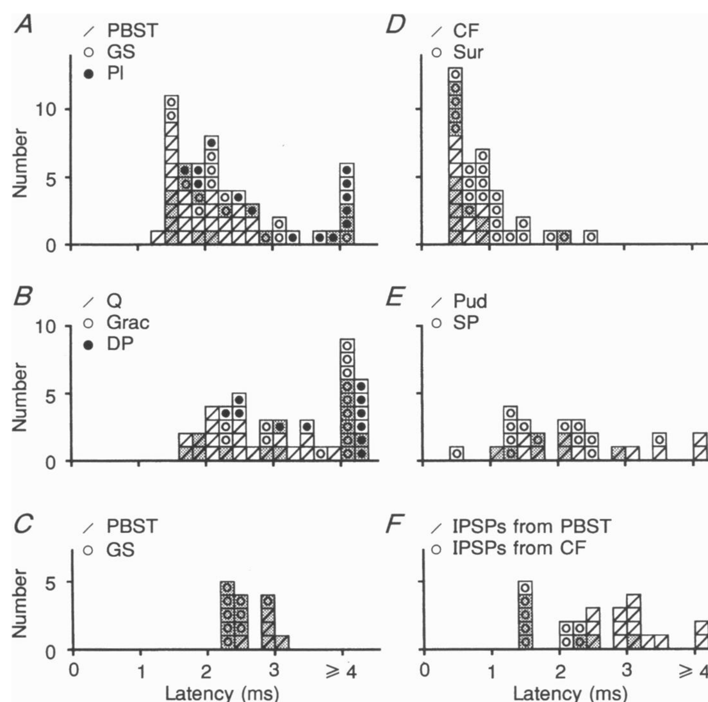

Figure 5. Latencies of EPSPs and IPSPs evoked in sacral ascending tract neurones
▩, SCT neurones; □, all other intracellularly recorded ipsilaterally projecting neurones. Symbols indicate PSPs evoked from different nerves as shown in the keys. *A* and *B*, latencies of EPSPs evoked by group II muscle afferents. *D* and *E*, latencies of EPSPs evoked by cutaneous afferents. *F*, latencies of IPSPs evoked from the PBST and CF nerves. *C*, for comparison, latencies of EPSPs evoked by group II afferents of the PBST and GS nerves in L6–L7 SCT neurones (from Harrison & Jankowska, 1984). Latencies considered compatible with a monosynaptic coupling are $< 1{\cdot}8$ ms for PBST, $< 2{\cdot}2$ ms for GS and Pl, $< 2{\cdot}6$ ms for Q, Grac and DP, and $< 1{\cdot}2$ ms for potentials evoked by cutaneous afferents (see Jankowska & Riddell, 1994 for reasoning).

EPSPs were demonstrated during the passage of a 10 nA depolarizing current (cf. records *B* with *A* and records *C* and *D* with records of Fig. 3*I* and *J*. The proportions of neurones in which various afferents evoked EPSPs which were followed by IPSPs are shown in Fig. 4, from which it can be seen that group II afferents of PBST and cutaneous afferents of CF and Sur were particularly effective. While IPSPs evoked by most afferents were combined with EPSPs, an exception to this was the actions of the afferents of SP, which produced IPSPs in all seven intracellularly recorded neurones and EPSPs in only two. Examples of IPSPs which were not preceded by EPSPs, or were combined with only small EPSPs, are shown in Figs 3*F* and *L*, and 6*E*.

The minimal latencies of IPSPs evoked by cutaneous afferents were 1·4–1·5 ms and of IPSPs evoked by group II muscle afferents 2·0–2·5 ms. These are less than 1 ms longer than the latencies of the earliest EPSPs recorded in the same neurones and, as in previous studies (Hongo *et al.* 1968; Harrison & Jankowska, 1984), are therefore considered to be evoked disynaptically.

Ipsilaterally projecting dorsal horn spinocerebellar tract neurones

In order to determine whether spinocerebellar tract neurones are among the ascending tract neurones in the dorsal horn of sacral segments, in two experiments electrodes were placed in the cerebellum at locations from which Clarke's column neurones could be antidromically activated by stimuli of less than 50 μA. These locations are indicated in Fig. 7*A* by open and filled triangles. Sacral neurones excited by group II muscle afferents and antidromically activated by stimulation of the lateral funiculus at the Th13 and/or C3 levels were then tested for antidromic activation by stimuli applied within the cerebellum. Stimuli were applied at various depths in a number of different tracks separated by 0·5–1·0 mm. The intensity of stimuli employed was varied between 0·2 and 0·5 mA, which would be likely to excite fibres of spinocerebellar neurones within a radius of 2–5 mm (see Gustafsson & Jankowska, 1976). However, in contrast to antidromically activated Clarke's column and midlumbar dorsal horn neurones, which were readily encountered following these procedures (both in this and previous studies; Edgley & Jankowska, 1988), only two of the eighteen sacral ascending neurones tested in this way were activated. It therefore appears that only a small proportion of sacral dorsal horn ascending tract neurones with group II input are likely to be ipsilaterally projecting spinocerebellar neurones. The sites from which the two sacral neurones could be antidromically activated at lowest stimulus intensities (between 22 and 80 μA in one experiment and 40 μA in another) are indicated in Fig. 7*A* by filled and open circles. Figure 7*B* shows in addition that the latencies of antidromic activation from the lowest threshold sites (along one of the electrode tracks) were about 1 ms longer than those from 1 mm above, an indication that slower conducting terminal branches were stimulated there (see Jankowska & Roberts, 1972).

Both spinocerebellar neurones were excited by group II afferents of PBST (at 1·9 and 2·4 ms latencies) and by afferents of CF and/or Sur (with 0·8 and 1·2 ms latencies,

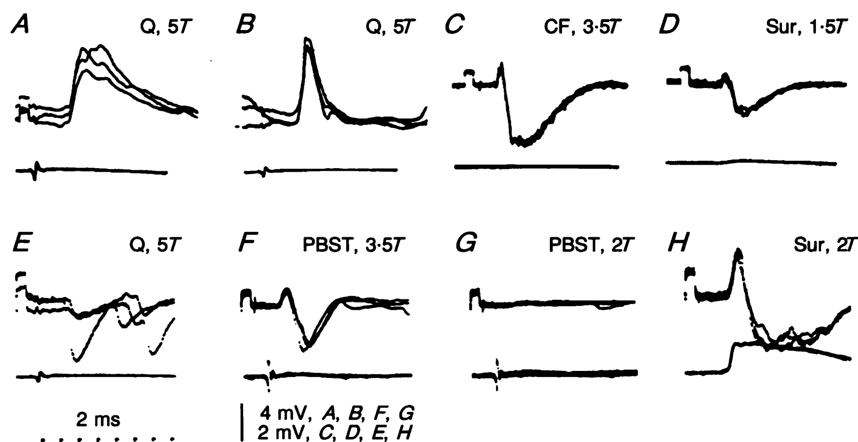

Figure 6. Examples of IPSPs evoked by stimulation of group II muscle afferents and cutaneous afferents in two SCT cells (*A–B* and *C–D*) and in an unidentified ascending tract cell (*E–H*)

The upper traces are of intracellular recordings and the lower traces recordings from the surface. *A* and *B* show PSPs evoked by activation of group II afferents of the Q nerve before (*A*) and during (*B*) the passage of a 10 nA depolarizing current to reveal an IPSP. All other records were made during the passage of a 10 nA depolarizing current. Records obtained prior to those in *C* and *D*, but without the passage of current, are shown in Fig. 3*I* and *J*. Note that IPSPs also followed EPSPs evoked from muscle and cutaneous afferents in the unidentified cell, and that those evoked from muscle afferents required stimuli supramaximal for group I afferents (cf. effects of stimuli 2*T* and 3·5*T* in *F* and *G*). Note also the large most probably unitary IPSPs in record *E*.

respectively; examples of records are shown in Fig. 7*C* and *D*), and therefore had a similar input to the majority of other sacral ascending tract neurones. The conduction velocities of their axons were 77 and 88 m s^{-1}. The location of their cell bodies is indicated in Fig. 1.

Unidentified ipsilaterally projecting ascending tract cells

Since 82% of adequately tested ipsilaterally ascending dorsal horn neurones were found to be SCT neurones (see above), the majority of other neurones which were antidromically activated by stimuli applied to the ipsilateral lateral funiculus at the Th13 and/or C3 level (but were not tested for more rostral projections) seem likely to have been SCT cells as well. As shown in Fig. 2*H*, when measured between the sacral and Th13 segments, the conduction velocities of these neurones (40–110 m s^{-1}) lay within a similar range (44–88 m s^{-1}) to the conduction velocities of identified SCT cells (Fig. 2*G*), though with a greater proportion of slower conducting neurones. Figure 4*A* shows, furthermore, that the proportions of neurones in which EPSPs were evoked by various group II muscle and cutaneous afferents were similar for both SCT cells and the population of sacral ascending tract neurones as a whole. This similarity also extended to the frequency with which monosynaptic EPSPs were followed by disynaptic IPSPs (Fig. 4*B* and examples in Fig. 6*E–H*) and to the latencies with which PSPs were evoked (summarized in Fig. 5*A–B* and *D–F*). On the basis of location, conduction velocity and the intracellularly recorded actions of peripheral afferents, the unidentified ascending tract neurones were therefore indistinguishable from the sample of SCT neurones.

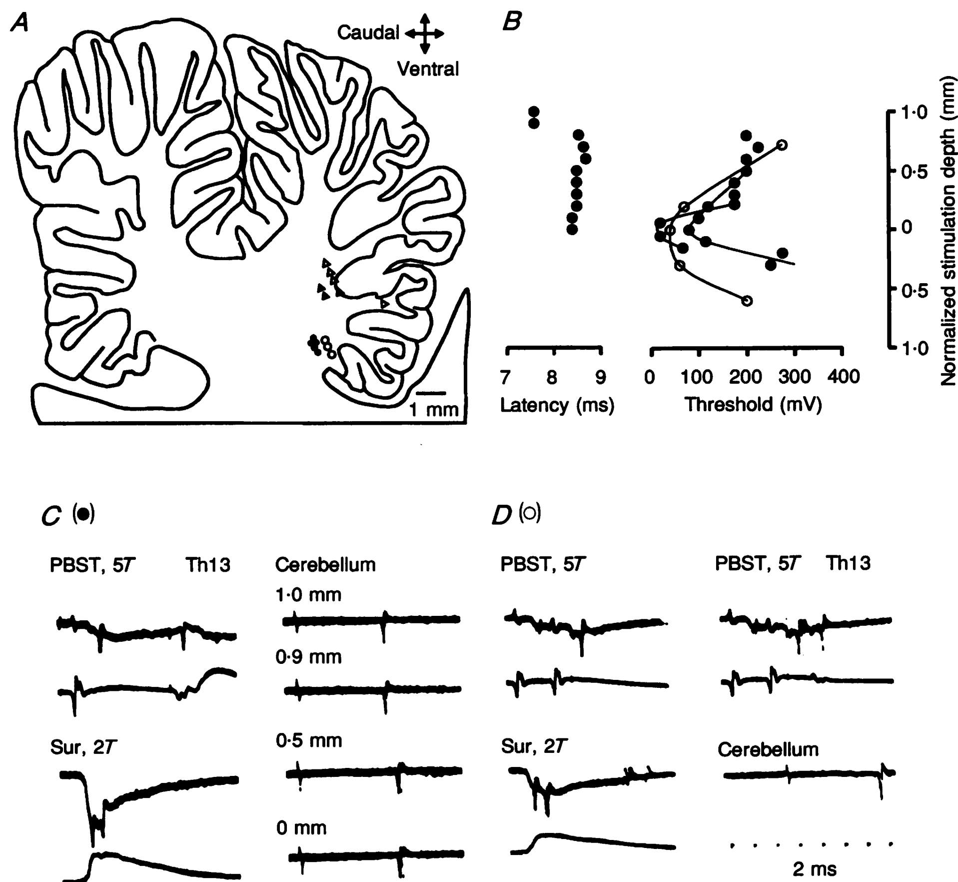

Figure 7. Sites of projection and examples of records from spinocerebellar tract neurones
A, sites at which stimuli ≤ 100 μA were followed by antidromic activation of neurones. Circles show the sites of activation of sacral dorsal horn neurones and triangles the sites from which Clarke's column neurones were activated. The filled symbols represent data from one experiment and open symbols the data from the other. The stimulation sites are superimposed on a drawing of a sagittal plane through the cerebellum about 3·0 mm lateral to the mid-line. ○, sites 3·5 mm lateral to the mid-line; △, sites 2·5 mm lateral to mid-line; ●, sites 3·0 and 4·0 mm lateral to the mid-line; ▲, sites 3·0 mm lateral to the mid-line. *B*, plots of threshold and latency of antidromic activation of the two sacral spinocerebellar neurones against normalized stimulation depth, 0 mm corresponding to the lowest thresholds. Two plots from separate tracks through the cerebellum are shown for one of the neurones. The symbols used are the same as in *A*. *C* and *D*, extracellular records from the neurones represented by filled and open circles in *A* and *B*, respectively.

Other neurones with an ascending projection

Four ipsilaterally projecting neurones were classified as long axoned propriospinal neurones since they were antidromically activated from the Th13 segment but did not respond to stimuli applied at the C3 level. The conduction velocities of these neurones were 49, 54, 66 and 69 m s^{-1}. All four were excited by group II muscle afferents and cutaneous afferents and were probably mono-synaptically activated, since they were discharged at latencies comparable to the shortest observed in sacral neurones.

Five of the seventy-three neurones (7 %) investigated in this study had axons which ascended in the contralateral lateral funiculus. These were tested only with stimuli applied at the Th13 level (for two neurones, above a transection of the dorsal columns) and so could have been either propriospinal or ascending tract neurones. They were excited by muscle group II and cutaneous afferents but at latencies (e.g. 2·2–3·7 ms from PBST; 1·2 ms from CF) too long to be compatible with a monosynaptic coupling.

DISCUSSION

Which types of ascending tract neurones process information from group II muscle afferents in the sacral segments?

The results of the present study show that in addition to interneurones (Jankowska & Riddell, 1994) ascending tract cells are amongst the dorsal horn neurones processing information from group II muscle afferents in the sacral segments of the spinal cord. The great majority of these neurones are likely to have terminated within the lateral cervical nucleus (and to belong therefore to the *spino-cervical tract*) since more than 80 % of the ipsilaterally projecting neurones adequately tested were readily activated by stimuli applied at the C3 level but not, or only at higher intensity, by stimuli applied at the C1 level. Though previous intracellular studies of SCT neurones have concentrated mainly on neurones in the lower lumbar rather than sacral segments (see below), retrograde labelling from the lateral cervical nucleus or dorsolateral funiculus using horseradish peroxidase (HRP) has shown that SCT neurones are present in the sacral segments (Craig, 1978; Brown, Fyffe, Noble, Rose & Snow, 1980; Enevoldson & Gordon, 1989*b*). Labelled neurones were numerous in the S1 segment and were also distributed throughout the S2–S4 segments, in the one cat (of Brown *et al.* 1980; see their Fig. 4*C*) in which segments caudal to S1 were inspected.

One difficulty in relating the present results to previous findings is that the segmental location of the sacral group II relay region differs somewhat between animals (as a result of variability in the degree of pre- and postfixation of the lumbosacral plexus; Romanes, 1951). The largest synaptic actions of group II afferents have, however, consistently been found to occur within the dorsal horn at locations overlying and just rostral to Onuf's nucleus (Jankowska & Riddell, 1993). This internal landmark has therefore been used in this and the accompanying report as a means of normalizing the positions of the recorded neurones (see Fig. 1). The distribution of neurones described in other studies will be subject to the same variability, but since in those reports the positions of neurones are related only to the spinal segments any comparisons must be considered approximate. As a guide, it can be seen from Fig. 1 of Jankowska & Riddell (1993) that the rostral end of Onuf's nucleus varies in location between the caudal part of the L7 and the rostral part of the S2 segments but is most often within the S1 segment. As can be deduced from Fig. 1, the neurones described in this report were therefore probably located mainly within the S1 segment.

In the midlumbar segments group II-activated *spino-cerebellar tract neurones* are quite commonly encountered within the dorsal horn (Edgley & Jankowska, 1988; Edgley & Gallimore, 1988). In contrast, in the sacral group II relay region, only two neurones (11 % of those tested) could be antidromically activated by stimuli applied in the cerebellum. These findings accord with those of anatomical studies of spinocerebellar pathways; following injections of HRP or other retrograde markers into the cerebellum, labelled neurones are only sparsely distributed in the dorsal horn of sacral segments and much fewer in number than in the midlumbar segments (see Figs 4 and 8 of Matsushita, Hosoya & Ikeda, 1979; Fig. 1 of Grant, 1982; Fig. 5 of Grant, Wiksten, Berkley & Aldskogius, 1982; Figs 2*D* and 4*D* of Xu & Grant, 1988). Interestingly, where hemisections of the spinal cord were performed in order to differentiate between ipsilaterally and contralaterally projecting neurones, similar numbers of both were present in the dorsal horn of the sacral segments (see Fig. 8 of Matsushita *et al.* 1979; Fig. 5 of Grant *et al.* 1982). It is possible, therefore, that the five contralaterally projecting neurones encountered in the present study (which were not tested for a projection to the cerebellum) were representatives of the dorsal horn spinocerebellar neurones with a crossed projection. Spinocerebellar neurones (most with axons that cross at the spinal level) are, however, more numerous in ventral parts of the sacral segments than in the dorsal horn. Some of these neurones (in the S1 segment) have been found to be monosynaptically excited and/or disynaptically inhibited by group II afferents (mainly of the PBST and GS nerves), but most lack the monosynaptic input from cutaneous afferents seen in the present sample of neurones (Grottel, Huber & Kowalski, 1991).

No evidence was found that *postsynaptic dorsal column neurones* are among sacral ascending tract neurones activated by group II afferents. Although retrograde labelling of neurones from the dorsal columns or dorsal column nuclei suggests that some at least are present in the sacral segments they may, as in more rostral segments, have a tendency to be concentrated in the medial half of the dorsal horn (Rustioni & Kaufman, 1977; Bennett,

Seltzer, Lu, Nishikawa & Dubner, 1983; Enevolson & Gordon, 1989*a*). Indeed, postsynaptic dorsal column neurones from which records were made intracellularly in the L7–S1 segments are reported to receive a weak monosynaptic input from group I afferents (Jankowska, Rastad & Zarzeki, 1979), which from the known distribution of group I actions in the sacral cord (see Fig. 5 of Jankowska & Riddell, 1993) would place them in deeper and more medial parts of the grey matter than generally explored in the present experiments. All but one of the neurones of the present sample were located within the lateral two-thirds of the dorsal horn.

The electrophysiological findings of the present study, supported by previous anatomical evidence, therefore lead to the conclusion that information from group II muscle and cutaneous afferents processed within the sacral segments is forwarded to supraspinal centres primarily via the spinocervical tract.

Comparison of the properties of SCT neurones in the sacral and more rostral segments

Some differences are apparent in the properties of the sacral SCT neurones recorded in this study and of the more rostrally located neurones of previous studies; most obviously with respect to the actions of group II muscle afferents. Sacral SCT neurones are strongly excited by group II afferents, particularly those of PBST and GS, which is sufficient to discharge the majority (two-thirds) of neurones. In contrast, in the lower lumbar segments (L6–L7), group II afferents (mainly of GS) have weaker actions on SCT neurones and affect a smaller proportion of neurones (Harrison & Jankowska, 1984). Furthermore, while EPSPs are evoked from group II afferents in sacral neurones at minimal latencies of 1·5–1·6 ms, those in L6–L7 neurones are evoked at minimal latencies of 2·2–2·6 ms (cf. Fig. 5*A* with *C*). Many sacral SCT neurones may therefore be excited monosynaptically by group II afferents, while only disynaptic actions on L6–L7 SCT neurones have so far been reported (Harrison & Jankowska, 1984). This difference in the actions of group II afferents on SCT neurones in different spinal segments seems in fact to closely reflect the distribution of the actions of these afferents within the lumbosacral spinal cord; much larger synaptic field potentials being evoked by group II afferents in the dorsal horn of the sacral (Jankowska & Riddell, 1993) than of the lower lumbar segments (Fu, Santini & Schomburg, 1974). Furthermore, it appears that SCT neurones located in the other main region in which group II afferents (of Q, Sart and DP muscles) have strong synaptic actions, the midlumbar segments (Edgley & Jankowska, 1987*a*, *b*), are also strongly and systematically activated by group II muscle afferents at latencies consistent with a monosynaptic connection (E. Jankowska, I. Hammar & Z. Szabo-Läckberg, unpublished data; work performed during the preparation of this manuscript).

Observations that the sacral SCT neurones were not excited by group I muscle afferents are consistent with previous reports that group I afferents are without influence on SCT neurones in the lower lumbar segments (Hongo *et al.* 1968; Hamman, Hong, Kniffki & Schmidt, 1978; Harrison & Jankowska, 1984).

The cutaneous input to SCT neurones is somatotopically organized such that neurones in different regions of the lumbosacral cord have receptive fields on different parts of the limb (Brown *et al.* 1980). It is therefore to be expected that neurones located in different segments of the spinal cord should be excited in the main by cutaneous afferents in different nerves, and this is indeed the case. The sacral SCT neurones were excited primarily by afferents of the CF and Sur nerves (innervating skin of the perineum, proximomedial parts of the thigh and lateral aspects of the foot; cf. Fig. 9 of Brown *et al.* 1980), while afferents of the SP nerve, which have predominantly an inhibitory action on sacral SCT neurones, provide the most potent excitatory input to SCT neurones in the lower lumbar segments (Hongo *et al.* 1968; Harrison & Jankowska, 1984).

Excitation evoked from cutaneous afferents was often followed by disynaptic IPSPs, as has been reported before for SCT neurones in the lower lumbar segments (Hongo *et al.* 1968). This finding is in keeping with observations that IPSPs can be evoked in some SCT neurones by natural stimulation of cutaneous receptors in skin within, or adjacent to, the excitatory receptive field (Hongo *et al.* 1968; Brown *et al.* 1987). Similarly, observations that postsynaptic inhibition of some SCT neurones can be induced by stimulation of skin remote from the excitatory receptive field (Hongo *et al.* 1968; Brown & Franz, 1969) is consistent with the predominantly inhibitory action of some cutaneous nerves on SCT neurones. In the case of sacral SCT neurones this appears to be afferents primarily in the SP nerve which produced IPSPs (largely without accompanying EPSPs) in all seven intracellularly recorded SCT neurones, while in SCT neurones of the lower lumbar segments Sur afferents are more often inhibitory (Hongo *et al.* 1968; Harrison & Jankowska, 1984).

Relations between ascending tract neurones and interneurones with group II input in the dorsal horn of the sacral segments

Despite the small samples of neurones involved, the patterns of input to the sacral ascending tract neurones investigated in this study and to the sacral interneurones described in the accompanying paper (Jankowska & Riddell, 1994) are remarkably similar (see Fig. 4). The somewhat larger proportions of ascending neurones with monosynaptic EPSPs from group II afferents of the GS and PL nerves and the somewhat larger proportions of interneurones with monosynaptic EPSPs evoked from Pud afferents are easily explained by the majority of ascending

tract neurones being located more rostrally than the interneurones. The two groups of neurones were also under inhibitory control of cutaneous and group II muscle afferents of the same nerves. In general then the two populations of neurones appear to process largely the same information. This similarity in the input to the two sets of neurones suggests that one function of sacral SCT neurones might be to monitor and convey to supraspinal neurones information on the state of activity in sacral interneuronal networks, as has been hypothesized by Lundberg (1971) for some spinocerebellar tract neurones.

There are several indications that sacral interneurones contribute to the excitation and inhibition of SCT neurones and in this way assist in the processing of information by these neurones. The strongest evidence relates to the disynaptic IPSPs evoked in SCT neurones by afferents in the PBST, CF and Sur nerves since this combination of afferents is a characteristic feature of the input to sacral interneurones (Jankowska & Riddell, 1994). Furthermore, more rostrally located interneurones are unlikely to mediate this inhibition, since the actions of PBST and CF afferents are much weaker outside the sacral segments. Other indications for the contribution of excitatory and inhibitory sacral interneurones are based on observations that di- and polysynaptic excitation of SCT neurones (Hongo & Koike, 1975; Brown *et al.* 1987) and also a long-lasting inhibition of these actions (Brown *et al.* 1987) can be evoked by cutaneous afferents. Since these actions are evoked from within the excitatory receptive fields of SCT neurones, both the interneurones responsible and the SCT neurones must be activated by the same afferents and the interneurones are therefore most probably located close to the neurones they affect.

The SCT as a pathway for the transmission of information from group II muscle afferents to the cortex

There is now compelling evidence that sensory signals from muscle afferents contribute to awareness of the movement and position of body parts (Burgess *et al.* 1982; Matthews, 1982). However, since muscle afferents from the lower limbs do not ascend beyond the thoracic segments (see Fern *et al.* 1988) any signals from these afferents which reach supraspinal centres must be conveyed by neurones of ascending tracts.

Information from group I muscle afferents is relayed to the somatosensory cortex by neurones in Clarke's column that, in addition to a projection to the cerebellum (which does not appear to be important for position sense; see Liebman & Levitt, 1973), also project via axon collaterals to the nucleus Z in the medulla (Landgren & Silfvenius, 1971; Johansson & Silfvenius, 1977). Neurones at this location project to neurones in the thalamus, which in turn influence neurones in the cerebral cortex. Recent evidence suggests that information from group II muscle afferents might also be relayed via nucleus Z, since axon collaterals of group II-activated midlumbar spinocerebellar neurones can be activated by electrical stimuli applied in this region (Asif & Edgley, 1992). However, this medullary relay would appear to be largely restricted to signals from group II muscle afferents of the particular muscles which excite midlumbar spinocerebellar neurones, since the present results show that group II-activated spinocerebellar neurones are scarce in the dorsal horn of the sacral segments and no such neurones have yet been found in the caudal lumbar segments.

The spinocervical–lemniscal system constitutes one of the main pathways by which sensory information from skin is conveyed to the forebrain (see Brown, 1981) and SCT neurones are very effectively activated by cutaneous input, a single impulse in a single hair afferent often being sufficient to discharge a SCT neurone (Brown *et al.* 1987). The present findings show that some spinocervical neurones process in addition information from group II muscle afferents. The secure activation of these neurones by electrical stimuli applied to muscle nerves suggests quite a strong group II input, though it will remain for future experiments to determine how SCT neurones respond to muscle stretches. The spinocervical–lemniscal system must thus be considered to convey to higher centres information from group II afferents, though it might be surprising that a system so specialized in the signalling of information from cutaneous receptors should also be concerned with the processing of information from muscle receptors. One functional advantage of this arrangement might be related to the high degree of somatotopic organization of the spinocervical–lemniscal pathway (Brown *et al.* 1980) and the close topographical relationship between the origin of skin and muscle input to sacral SCT neurones found in this study (the CF nerve, for example, innervates skin overlying the PBST muscle). The organization of group II muscle and cutaneous afferent input to neurones of the SCT might thus constitute the first stage in the integration of information from muscle, skin and joint receptors which is the basis for a sense of position of a given joint or a body part.

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