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A RELAY FOR INPUT FROM GROUP II MUSCLE AFFERENTS IN SACRAL SEGMENTS OF THE CAT SPINAL CORD

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SUMMARY

1. A neuronal relay for input from group II afferents of hindlimb muscle nerves has been found in the previously little explored sacral segments of the cat spinal cord.

2. Electrical stimulation of group II muscle afferents of a number of nerves evoked negative potentials on the surface (cord dorsum potentials) and population postsynaptic potentials (field potentials) within the sacral segments. The largest potentials were evoked by stimulation of the posterior biceps–semitendinosus and triceps surae nerves which evoke much smaller potentials in other segments. Group II afferents of other nerves, notably those which have their main relay within the middle lumbar segments, were much less effective.

3. The sites at which cord dorsum and field potentials evoked by group II muscle afferents were recorded varied in relation to the external topography of the L7–S2 spinal segments but were consistent in their location relative to the pudendal motor nucleus (Onuf's nucleus). Potentials evoked by group II afferents of the posterior biceps and semitendinosus nerves peaked at a level corresponding to the rostral half of Onuf's nucleus and potentials evoked by afferents of the gastrocnemius nerves peaked just rostral to this nucleus. The largest field potentials (of 0·5–1·0 mV) were recorded within the dorsal horn. Field potentials in the intermediate zone were much smaller ($< 0{\cdot}3$ mV) and were seen less frequently.

4. Evidence was obtained that the dorsal horn field potentials are to a great extent evoked monosynaptically by the fast conducting fraction of group II muscle afferents: (i) they were evoked at short latencies (2·4–2·7 ms from the stimulus; 1·3–1·7 ms from group I components of afferent volleys and 0·5–0·7 ms from group II components of these volleys), (ii) the conduction times of impulses in the fastest conducting fraction of group II afferents, between the sacral segments (where these impulses were induced by intraspinal stimuli) and the peripheral nerves, were only about 0·5 ms shorter than the latencies of field potentials recorded at the site of intraspinal stimulation and evoked by stimulation of the same peripheral nerves and, (iii) the field potentials followed repetitive stimuli without temporal facilitation.

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5. Negative cord dorsum and field potentials were also evoked by small stretches of the semitendinosus and triceps surae muscles. Although they were smaller than potentials evoked by electrical stimulation of sensory fibres and appeared at longer latencies, their presence is consistent with a contribution of muscle spindle afferents to the actions of group II muscle afferents within the sacral segments.

6. The study leads to the conclusion that there are neurones within the sacral segments that mediate the actions of group II afferents primarily of posterior biceps and semitendinosus and gastrocnemius–soleus. Together with previous observations on the actions of group II muscle afferents in other spinal segments, the results of this study suggest that neurones in different segments of the spinal cord are specialized in processing information from group II afferents of different muscles.

INTRODUCTION

Several kinds of observation have provided evidence that group II afferents of hindlimb muscles terminate within the S1 to caudal thoracic segments and make synaptic contacts with neurones in laminae IV–IX of Rexed (1954). For instance, single muscle spindle secondaries labelled by intra-axonal injection of horseradish peroxidase have been found to terminate within laminae IV–IX of the L6 and L7 segments (Fyffe, 1979; Hongo, Kudo, Yamashita, Ishizuka & Mannen, 1981; Ishizuka, Hongo, Kudo, Sasaki, Yamashita & Mannen, 1985; Hoheisel, Lehmann-Willenbrock & Mense, 1989; Hongo, 1992) and group II muscle afferent fibres have been activated by intraspinal stimuli applied at segmental levels from S1 to Th13 (Eccles, Schmidt & Willis, 1963; Carpenter, Lundberg & Norrsell, 1963; Fu & Schomburg, 1974; Lundberg, Malmgren & Schomburg, 1987*a*; Edgley & Jankowska, 1987*a*; Fern, Harrison & Riddell, 1988; Jimenez, Rudomin & Solodkin, 1988; Harrison & Jankowska, 1989; Riddell, Jankowska & Eide, 1992). Group II muscle afferent fibres have also been found to have direct contacts with neurones within the dorsal horn, the intermediate zone, Clarke's column and motor nuclei within the S1 to L3 segments (Coombs, Curtis & Landgren, 1956; Eccles, Oscarsson & Willis, 1961; Fu, Santini & Schomburg, 1974; Kirkwood & Sears, 1975; Stauffer, Watt, Taylor, Reinking & Stuart, 1976; Lundberg, Malmgren & Schomburg, 1977, 1987*a*,*b*; Munson, Fleshman & Sypert, 1980; Edgley & Jankowska, 1987*b*, 1988; Jankowska & Noga, 1990; for review see Jankowska, 1992).

However, group II afferents of different muscles appear to have preferred projection areas. For instance, neurones in the dorsal horn and the intermediate zone of the L3 and L4 segments are primarily contacted by group II afferents of the quadriceps, sartorius, gracilis and pretibial flexor muscles (Edgley & Jankowska, 1987*b*, 1988) while dorsal spinocerebellar tract neurones located in Clarke's column of the same segments are contacted not only by these afferents but also by afferents of the hamstring, triceps surae and plantaris nerves (Eccles *et al.* 1961). Neurones of the L7 segment (both in the dorsal horn and in the intermediate zone) have, on the other hand, been found to be contacted primarily by group II afferents of the triceps surae (Fu & Schomburg, 1974; Fu *et al.* 1974; Lundberg *et al.* 1987*b*). A further differentiation of the projection areas of group II afferents has been revealed in the present study. It will be shown that group II afferents of the

semitendinosus and triceps surae muscles produce much larger synaptic actions in the S1 and S2 segments than in more rostral segments of the spinal cord (Fu *et al.* 1974; Edgley & Jankowska, 1987*a*,*b*), suggesting that the preferred relay area of these afferents is located in the sacral spinal cord. The properties of neurones with group II input in the sacral segments will be described in a forthcoming paper. Preliminary results have been briefly reported (Jankowska & Riddell, 1992*a*,*b*).

METHODS

Preparation

Experiments were performed on seventeen deeply anaesthetized cats weighing 2·5–3·6 kg. Anaesthesia was induced with sodium pentobarbitone (40 mg/kg I.P.) and maintained with chloralose (added when needed up to 50 mg/kg). The adequacy of the anaesthesia was verified by monitoring withdrawal and corneal reflexes during the surgery and the diameter of the pupils and blood pressure during the experiments when the animals were paralysed with gallamine triethiodide and artificially ventilated. The mean blood pressure was kept above 90 (usually 110–130) mmHg and the end-tidal CO_2 was maintained close to 4 % by adjusting the parameters of the artificial respiration and the rate of infusion of a 100 mM solution of sodium bicarbonate containing 5 % glucose. The animals' core temperature was maintained at 37–38 °C and that in the paraffin pools at 35–37 °C.

A number of hindlimb peripheral nerves were dissected and mounted on electrodes. These routinely included: the quadriceps (Q), posterior biceps (PB), semitendinosus (ST), posterior biceps together with semitendinosus (PBST), anterior biceps–semimembranosus (ABSm), medial gastrocnemius (MG), lateral gastrocnemius–soleus (LG–S), soleus (S) medial and lateral gastrocnemius together with 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), superficial peroneal (SP) and the posterior knee joint (J) nerves. In some experiments the sartorius (Sart), gracilis (Grac), adductor femoris (AF), peroneus longus (PerL), popliteus (Popl), flexor digitorum longus (FDL, dissected free from the interosseous nerve), the remaining part of the tibial (Tib), saphenus (Saph), pudendal (Pud) and/or the cutaneous femoris (CF) nerves were also dissected.

The spinal cord was exposed by laminectomy from the fourth lumbar to the sacral segments. The dura was opened over all these segments. The L7 and S1 ventral roots were sectioned in five of the experiments.

Recording and stimulation procedures

To record cord dorsum potentials silver ball electrodes were placed about 0·5 mm medial and in some experiments 1 mm lateral of the lateral sulcus, i.e. on the dorsal columns and the dorsal part of the lateral funiculus respectively. These electrodes were moved along the dorsal columns or the lateral funiculus in 1 or 2 mm steps (see first section of Results).

Records of field potentials were obtained with glass microelectrodes filled with 2 M NaCl or potassium citrate solution (1–2 μm tip diameter, 2–4 MΩ resistance). The electrodes were introduced through the dorsal columns at an angle of 20–40 deg from the vertical, with the electrode tip directed laterally, and 10 deg from the vertical, with the tip directed rostrally. When recording field potentials, afferent volleys were routinely recorded with cord dorsum electrodes placed a few millimetres rostral of the recording site. Records were photographed and averaged on line (5 μs per address time resolution, averages of 16–64 individual potentials).

In order to activate the central terminals of afferent fibres intraspinal stimuli (0·2 ms duration, up to 5 μA) were delivered via glass microelectrodes filled with 2 M NaCl solution (1–2 μm tip diameter, 1–2 MΩ resistance) within regions of the dorsal horn in which field potentials were recorded via the same electrodes (5 experiments). Nerve impulses induced by such stimuli (in the centrifugal direction) were recorded from the cut distal ends of the longest, or one of the short branches of the ST nerve and from two or three natural branches of the LG nerve. In order to induce impulses in the same nerves in the centripetal direction, the nerves were stimulated via pairs of electrodes which were in contact with the nerve proximal to the recording electrodes (for details see the small print paragraph in Results).

Peripheral nerves were stimulated with 0·1 ms rectangular current pulses, applied singly or in trains. Stimulus strengths are expressed relative to threshold (T) for the most excitable afferents

in the nerve, as detected by recording from the dorsal root entry zone, or from the sciatic nerve. In muscle nerves there is considerable overlap in the peripheral thresholds of the least excitable afferents in the group I range and the most excitable fibres in the group II range. Depending on the particular nerve stimulated, activation of all group I afferents may require stimuli of up to about $2T$ while group II afferents may begin to be recruited by stimuli of $1{\cdot}5T$ and the great majority are activated by stimuli of $5T$ (see especially Jack, 1978; Ellaway, Murphy & Tripathi, 1982; Lundberg *et al.* 1987*a*). Only effects appearing or growing in amplitude with stimuli between $2T$ and $5T$ were, therefore, attributed to the actions of group II afferents.

Histological control

In order to define the intraspinal location of recording and stimulation sites glass electrodes were left in each of the explored regions of the spinal cord. The spinal cord was fixed by intra-arterial injection of about 300 ml of 4% formalin in phosphate buffer and by subsequent immersion in the same solution. Transverse sections 200 μm thick were cut on a vibratome (as close as possible to the plane of the electrode insertion) and stained with Cresyl Violet. The electrode tracks were located and the recording and stimulation sites along these tracks were then defined from the known depths of the electrode tips. The rostrocaudal levels of the recording sites were defined not only with respect to the level of entry of the L7, S1 and S2 dorsal roots but also with respect to the pudendal motor nucleus (the feline homologue of Onuf's nucleus; Sato, Mizuno & Konishi, 1978; Ueyama, Mizuno, Nomura, Konishi, Itoh & Arakawa, 1984; Thor, Morgan, Nadelhaft, Houston & DeGroat, 1989; Beattie, Li, Leedy & Bresnahan, 1990). This procedure was followed in view of the considerable differences in the location of spinal neurones and in the level of entry of afferent fibres in relation to the spinal segments in pre- and postfixed spinal cords (see Romanes, 1951). The compact column of small neurones, with prominent Nissl bodies, which form the pudendal nucleus was clearly seen at the lateral border of the ventral horn, half- way between the dorsally located lateral and medial popliteal motor nuclei and ventrally located tail and levator ani motoneurones (see Rexed, 1954, Figs 26 and 43; Romanes, 1951; Sato *et al.* 1978; Jankowska, Padel & Zarzecki, 1978; Mackel, 1979). In the present study the rostral border of Onuf's nucleus was defined as the most rostral section containing the small neurones of the pudendal motor column without the much larger neurones which appeared in between them in more rostral sections. These large neurones are most probably the caudalmost ST and/or MG motoneurones since retrogradely labelled motoneurones were seen at this location after injection of wheat germ agglutinin–horseradish peroxidase (WGA–HRP) into the ST and MG nerves (S.A. Edgley, E. Jankowska & B. Skoog, unpublished observations, see also Romanes, 1951). In Fig. 1 *A* and *B* are shown cross-sections of the spinal cord at two levels of Onuf's nucleus which is indicated by the arrows. The diagrams in *C* relate this nucleus to the L7, S1 and S2 segments in eleven of the cats used in this study. In relating the level of Onuf's nucleus to surface features a correction has been made to take account of the fact that sections were cut at an angle of about 10 deg from the vertical. Since Onuf's nucleus is located at a depth of about 2·5 mm from the surface, the sections from which the level of Onuf's nucleus was determined have been related to the surface 0·4 mm more rostral. The figure shows that Onuf's nucleus had a length of some 3–4 mm but varied in its location relative to the different spinal segments. In the most extreme cases it was confined to the S2 segment, or extended as far rostrally as the caudal part of the L7 segment. In order to normalize the topography of the investigated neurones we have, therefore, used the rostral border of Onuf's nucleus (as defined above) as a reference level. The location of the recording sites will accordingly be expressed in millimetres caudal or rostral to this level.

RESULTS

Surface potentials

Distinct negative potentials follow incoming volleys in records from the surface of the spinal cord (cord dorsum potentials) in the L3–L5 segments when group II afferents of the Q, Sart and DP nerves are stimulated electrically (Edgley & Jankowska, 1987*a*). These potentials are evoked in parallel with negative population postsynaptic potentials (PSPs; field potentials) in the dorsal horn and the intermediate zone of the grey matter and most closely reflect those in the dorsal horn. In contrast, group II afferents of these and other muscle nerves, including

PBST, GS and Pl produce much smaller, or negligible cord dorsum and field potentials in the L6–L7 segments (Bernhard, 1953; Fu *et al.* 1974; Edgley & Jankowska, 1987 *a*). These observations suggest that the neurones contacted by group II afferents of these nerves might be spread out over larger parts of the grey

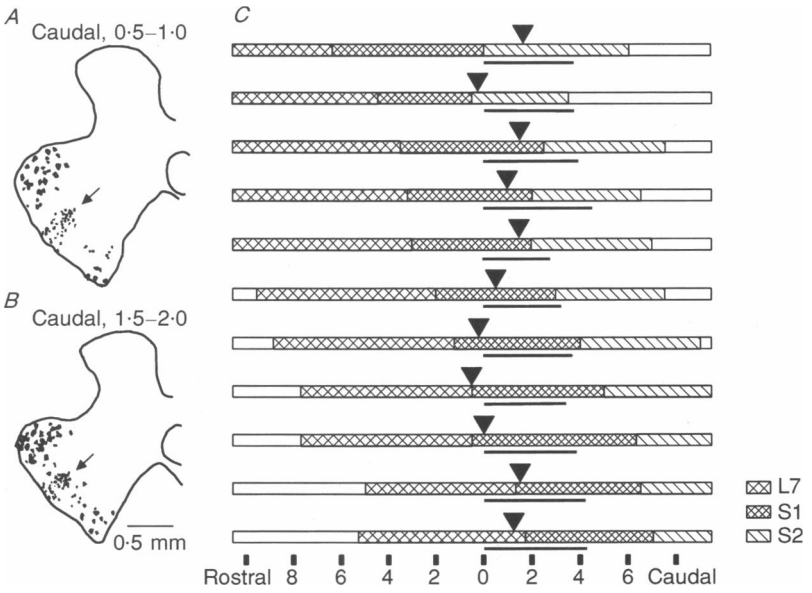

Fig. 1. Topographic relations between the pudendal (Onuf's) motor nucleus, L7–S2 spinal segments and the maximal cord dorsum potentials evoked by group II afferents of the PBST nerve. Each of the rows in *C* shows these relations in one of eleven cats. The extent of the spinal segments L7, S1 and S2 is indicated by the symbols shown in the key and the extent of Onuf's nucleus is indicated by a filled horizontal bar. Arrowheads show where the largest cord dorsum potentials produced by stimulation of the PBST or ST nerve at 5*T* were recorded. The scale indicates distances in millimetres, rostral and caudal of the rostral border of Onuf's nucleus (see Methods). In *A* and *B* are cross-sections of the spinal cord of one of the animals at levels 0·5–1·0 and 1·5–2·0 mm caudal of the rostral border of the pudendal motor nucleus. Nerve cells at the location of the tibial (dorsal), pudendal (arrowed) and levator ani (ventral) motor nuclei from three 200 μm thick sections have been superimposed.

matter than those with input from the Q, Sart, and DP nerves in midlumbar segments or that they might be clustered at previously unrevealed locations. In order to investigate this latter possibility the spinal cord was searched for potentials evoked by group II afferents at more caudal locations than before.

Previous observations that small or marginal cord dorsum potentials are evoked by group II afferents of muscle nerves within the L6–L7 segments were confirmed. When stimuli applied to muscle nerves were increased from 2 to 5*T* the largest addition to the surface potentials produced did not exceed 20–25 μV. Such potentials were small in comparison to the cord dorsum potentials evoked from the Q and DP nerves in the L4–L5 segments in the same experiments (30–90 μV; means 60 ± 18 μV, $n = 8$ and 56 ± 20 μV, $n = 8$ respectively). However, large cord dorsum potentials were evoked caudal to the lumbosacral enlargement, from group

II afferents of the PBST nerve in particular (40–85 μV; mean 52 μV, $n = 13$; see Figs 2*A*,*B* and 3*B*). The stimulus intensity needed to evoke such potentials was always supramaximal for group I afferent volleys and the potentials reached a maximum amplitude when evoked by stimuli of 4–5*T*. In Fig. 2*A* the averaged

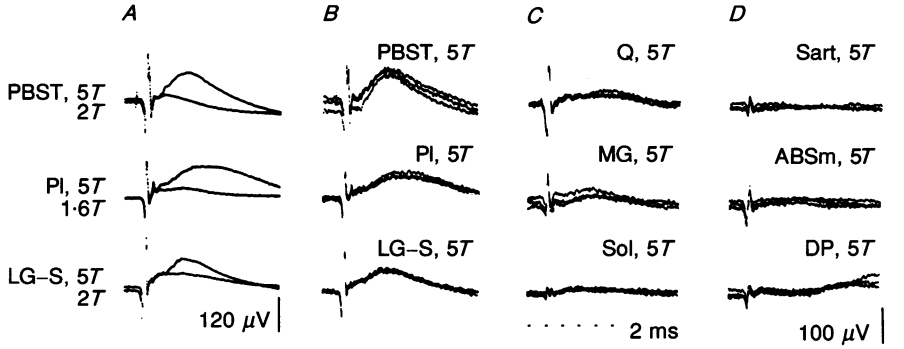

Fig. 2. Examples of potentials recorded from the surface of the spinal cord 1 mm caudal to the rostral border of Onuf's nucleus (in the S1 segment) following stimuli of 5*T* applied to the indicated muscle nerves; all records are from the same experiment. *A* and *B* show potentials evoked by stimulation of the most effective nerves, while *C* and *D* show examples of records in which potentials of group II origin were much smaller or absent. In *A* the averages of sixteen potentials evoked by stimuli of 5*T* (including those in *B*) are superimposed on potentials evoked by stimuli which were maximal for group I volleys, and subthreshold for the majority of group II afferents; the difference between them is thus attributable to the actions of group II afferents. The time calibration applies to both single sweep and averaged records while separate voltage calibrations are indicated.

records of potentials evoked by stimuli 2*T* (supramaximal for group I afferents and near-threshold for group II afferents) and 5*T* (near-maximal for group II afferents) are superimposed, those of larger amplitude being evoked by the stronger stimuli. The difference between the records therefore represents the net effect of group II afferents. The potentials were evoked with latencies of 1·5–2·2 ms from group I volleys which are comparable to, or shorter than those of similar potentials recorded in the midlumbar segments (2·0–2·2 ms for Q potentials and 2·5–2·9 ms for DP potentials).

Of the wide range of muscle nerves tested for their actions in the sacral region, group II afferents of the nerves to PBST, or ST alone, consistently produced the largest potentials; only a restricted number of other nerves evoked cord dorsum potentials at the same level. The largest of these were evoked from the GS and Pl nerves (means 38 ± 30 μV, $n = 10$ and 30 ± 33 μV, $n = 9$; respectively), as illustrated in Fig. 2*A* and *B*. Stimulation of Q and Grac and of the PB, MG and Sol nerves alone usually had a much smaller effect (potentials of $\leqslant 10$ V, as exemplified in Fig. 2*C*) while stimulation of the Sart, AF, ABSm, FDL, DP and PerL nerves was practically without effect (as exemplified in Fig. 2*D*).

The locations at which group II afferents of PBST induced the largest cord dorsum potentials showed no fixed relation to the L7, S1 or S2 segments, as defined by the entry of their respective dorsal roots. They were, however, closely related to the levels within which Onuf's nucleus was located. Figure 1*C* shows that maximal surface potentials evoked by stimulation of the PBST nerve (indicated by

arrowheads) were regularly found close to (within 2 mm) the rostral border of this nucleus. Figure 3*A* shows, in addition, that the potentials declined to about two-thirds of their maximal amplitude within about 1 mm from the borders of Onuf's nucleus, although they could be detected over distances of more than 10 mm.

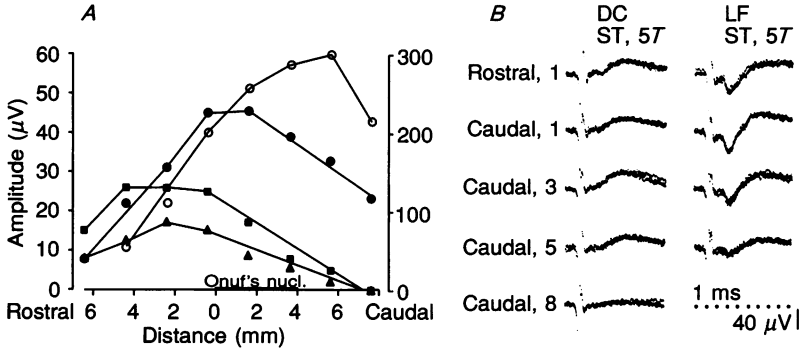

Fig. 3. Distribution of potentials of group II origin recorded at the surface of the spinal cord in relation to Onuf's nucleus. *A*, mean amplitudes (left-hand ordinate) of potentials evoked by stimuli of 5*T* applied to the PBST (●, $n = 11$), GS (■, $n = 7$) and Pl (▲, $n = 7$) nerves plotted against the distances caudal (C) and rostral (R) to the rostral border of Onuf's nucleus, as in Fig. 1. For comparison the rostrocaudal distribution of potentials evoked by stimuli of 2*T* applied to the pudendal nerve (○, $n = 2$; right-hand ordinate) is also shown. *B* and *C*, comparison of potentials (3 superimposed sweeps) recorded from the surface of the dorsal columns (DC) and the lateral funiculus (LF) between 1 mm rostral and 8 mm caudal of the rostral border of Onuf's nucleus.

Maximal potentials from the GS and Pl nerves were evoked about 2 mm more rostrally than those evoked from the PBST nerve while the maximal potentials evoked from the Pud nerve were evoked 3–4 mm more caudally.

Potentials of group II origin, evoked upon stimulation of the PBST nerve, were also seen in records from the surface of the lateral funiculus (see Fig. 3). These potentials were similar to those recorded from the cord dorsum in that they were evoked by stimuli of 5*T* but not 2*T* and their amplitude declined in parallel with that of cord dorsum potentials caudal to Onuf's nucleus. They nevertheless differed in configuration, the first phase of the potentials being positive rather than negative and its latency 0·2–0·4 ms shorter than that of potentials recorded at an equivalent level on the cord dorsum.

Field potentials

Following stimulation of the PBST and GS nerves at 5*T*, distinct field potentials were regularly recorded at locations corresponding to those over which the largest cord dorsum potentials were induced from these nerves (see Figs 4*A* and *B* and 6*A*). As illustrated in Fig. 6*A*, the appearance and increase in amplitude of the field potentials following graded increases of stimulus strength were clearly related to the range over which increasing proportions of group II afferents should be recruited. Traces of the field potentials usually appeared at stimulus intensities of 1·8–2·0*T* which activate only the most excitable of group II afferents (Jack, 1978; see Methods) and which are often, as in this example, maximal or close to maximal

for group I afferents. Stimuli of 3–5T which should activate the majority of group II afferents produced much larger potentials but there was little further increase in amplitude at stimulus strengths above 5T which begin to recruit group III afferents. Further evidence that these field potentials originate from group II

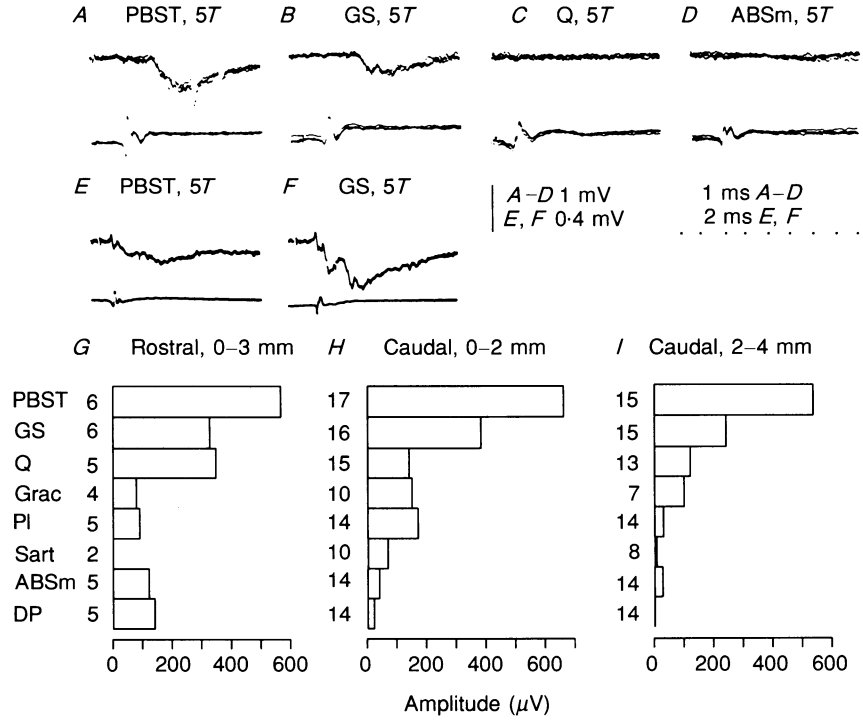

Fig. 4. A–F show examples of field potentials (upper traces) recorded in the same segment (S2) as Onuf's nucleus; lower traces are from the cord dorsum. A and B show field potentials evoked in the dorsal horn from the PBST and GS nerves and C and D the contrasting lack of effect, at the same sites, of stimuli applied to other nerves. E and F show field potentials evoked in the intermediate region from the PBST and GS nerves. In the records in A–D several single sweeps records are superimposed and in E and F are averages of sixteen such records. G–I, histograms of the mean maximal amplitudes of field potentials evoked by stimuli of 5T applied to the nerves listed to the left. The means are calculated from the largest potentials encountered in electrode tracks through regions 0–3 mm rostral, 0–2 mm caudal and 2–4 mm caudal of the rostral border of Onuf's nucleus. Numbers of tracks are listed to the left.

afferents is provided by their latencies which corresponded to those expected of actions mediated by group II afferents and were always longer than those of any field potentials evoked in the same segments by stimuli of less than 1·5T, i.e. group I afferents (see below).

Distribution

Field potentials of group II origin were evoked both in the dorsal horn (laminae IV–V) and in the intermediate zone (laminae V–VI) in a region overlying and extending slightly beyond the pudendal motor nucleus. Figure 5 shows the distribution of field potentials evoked from the PBST and GS nerves in one of three

experiments in which their locations were systematically mapped. The mapping involved recording field potentials evoked by stimuli of $2T$ and $5T$ at 100 or 200 μm intervals along each electrode track. Up to five tracks were made at varying angles with the same surface entry point, so that most of the dorsal horn and intermediate

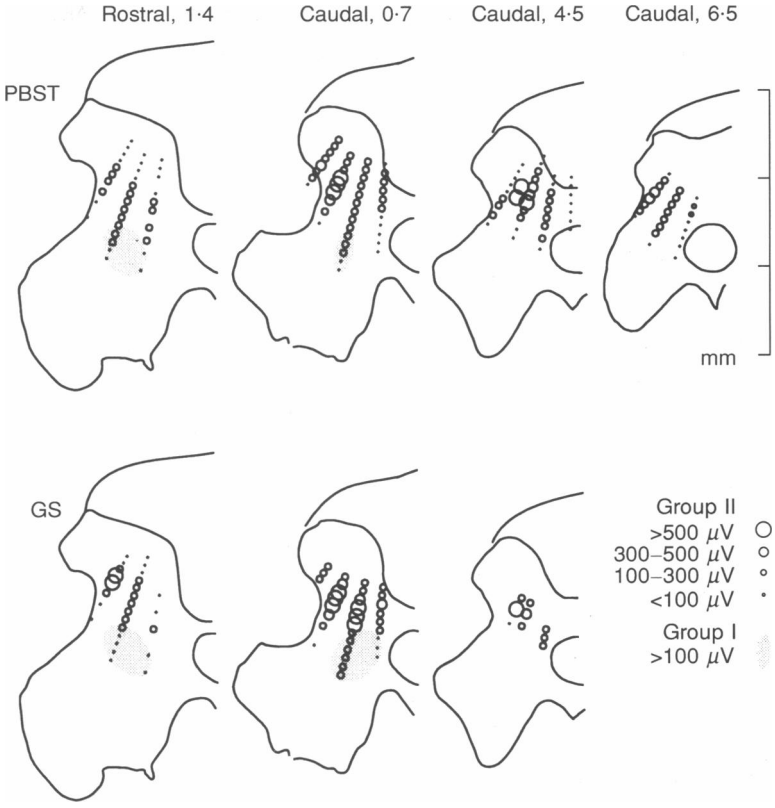

Fig. 5. Distribution of group II field potentials (circles) evoked from the PBST and GS nerves in frontal planes 10 deg from the vertical (see Methods). The potentials were mapped at four rostrocaudal levels in the L7 and S1 segments, 1·4 mm rostral and 0·7, 4·5 and 6·5 mm caudal of the rostral border of Onuf's nucleus. The potentials were recorded at 100 or 200 μm intervals along three or four electrode tracks at increasing angles. The amplitudes of the potentials at each site are indicated by the sizes of the circles (see key). The areas within which field potentials evoked by group II afferents were preceded by field potentials of group I origin $\geqslant$ 100 μV in amplitude are shaded.

grey matter was explored. The figure shows that the dorsal horn field potentials were much larger than those in the intermediate zone and that the largest potentials were found within the lateral two-thirds of the dorsal horn, about 1·2–1·6 mm ventral to the surface of the spinal cord and about 0·2 mm dorsal to the dorsal edge of the central canal. These areas were usually reached at angles of 20–30 deg (the tip of the electrode directed laterally) with entry points 0·4–0·6 mm from the midline. Rostrocaudally the largest field potentials from PBST were evoked over about a 4 mm length of the spinal cord containing Onuf's nucleus, and smaller field potentials within an additional 1–2 mm rostral and caudal of this

nucleus. The mean maximum amplitude of potentials recorded at levels equivalent to the rostral half of Onuf's nucleus was 650 μV (see Fig. 4 *G–I*) and that of the largest potentials amounted to 1 mV (see Fig. 6 *A*). Field potentials evoked by GS afferents were usually largest just medial to the largest potentials produced by PBST afferents; they were distributed over a similar rostrocaudal region but shifted some 1–2 mm more rostrally. The mean maximum amplitudes of group II field potentials evoked from GS were about half as large as of potentials evoked from PBST, both at levels rostral to Onuf's nucleus (Fig. 4 *G*) and equivalent to it (Fig. 4 *H* and *I*). In some experiments, however, the largest group II potentials evoked from GS (900 μV) were nearly as large as those from PBST.

Intermediate zone field potentials evoked by group II afferents were most often found close to the rostral border of Onuf's nucleus and at more medial locations than the dorsal horn field potentials (see Fig. 5; shaded regions). They were often preceded by field potentials of group I origin, the latter appearing at lower stimulus strengths (below 1·5*T*) and shorter latencies (0·6–1·0 ms) from group I volleys. Rostral to Onuf's nucleus such group I field potentials became much larger than group II field potentials (as described by Fu *et al.* 1974), while at middle and caudal levels of Onuf's nucleus only traces of these potentials were seen. The amplitudes of intermediate zone field potentials of group II origin did not exceed 300 μV. Examples are shown in Fig. 4 *E* and *F*.

Nerve origin

In contrast to the actions of afferents of PBST and GS, other muscle nerves were much less effective in inducing field potentials at the level of Onuf's nucleus; in many electrode tracks, particularly at levels equivalent to the caudal half of Onuf's nucleus, potentials were induced exclusively by PBST and GS (see Fig. 4 *A–D*). Potentials evoked by group II afferents of other nerves were most in evidence around the rostral border of Onuf's nucleus but were always less frequently encountered, recorded over a smaller range of depths and of smaller amplitudes than potentials evoked from PBST or GS. Figure 4 *E–G*, shows the mean maximum amplitudes of field potentials evoked from a range of nerves, the actions of which were recorded at the same sites in the dorsal horn as potentials produced by PBST or GS.

Field potentials of large amplitude were, however, induced by low threshold cutaneous afferents at the same locations in the dorsal horn at which group II afferents of PBST and GS evoked potentials. Cutaneous afferents were most effective at levels equivalent and rostral to the rostral end of Onuf's nucleus. Of the various nerves tested afferents of the CF and Sur nerve induced much larger potentials than those of SP and Saph. The mean maximum amplitudes of potentials recorded in electrode tracks between 2 mm rostral and 2 mm caudal of the rostral border of Onuf's nucleus were; CF, 2135 μV ($n = 10$); Sur, 1477 μV ($n = 12$); SP, 271 μV ($n = 14$) and Saph, 312 μV ($n = 5$). These observations are in good agreement with the distribution of surface potentials produced by afferents of these nerves (Bernhard, 1953).

Stimulation of the pudendal nerve which contains sensory afferents from cutaneous receptors in skin of the genitalia and the perineal area as well as afferents from mechanoreceptors associated with the urethra and rectum

(Barrington, 1931; Bors, 1952; Martin, Fletcher & Bradley, 1974) also induced large field potentials at locations where potentials produced by PBST and GS were recorded. The mean maximal amplitude of potentials of pudendal origin at the level of Onuf's nucleus was 1230 μV ($n = 12$) but they were largest within the region

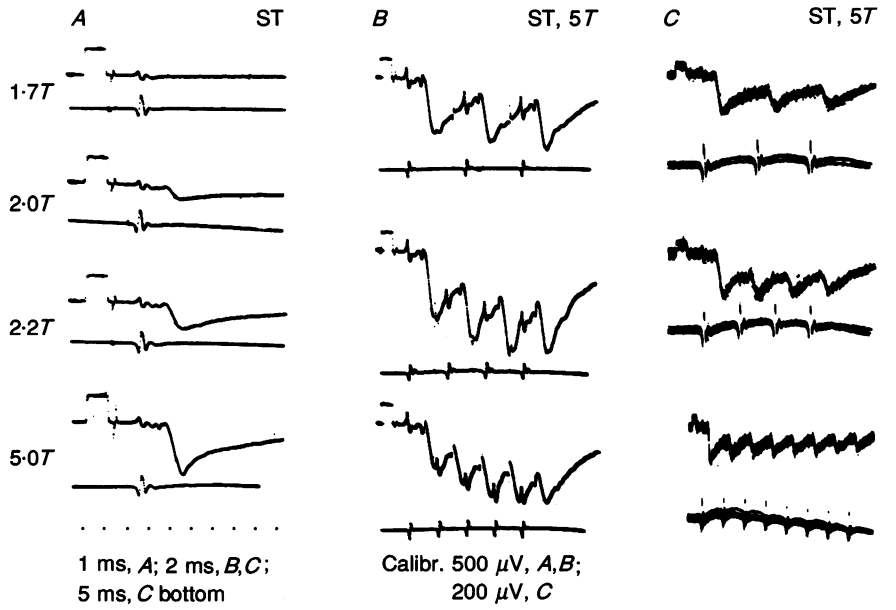

Fig. 6. Examples of group II field potentials evoked by repetitive stimuli. *A*, averaged records from the dorsal horn (upper traces) and from the surface of the spinal cord (lower traces) 0·9 mm caudal of the rostral border of Onuf's nucleus; these records illustrate that field potentials were evoked only by stimuli supramaximal for group I afferents. *B*, averages of recordings made at the same location as in *A* following stimuli of increasing frequencies (300, 400 and 600 Hz). *C*, superimposed single sweep records of group II field potentials evoked by repetitive stimuli in another experiment. Note that each of the stimuli, including those in longer trains, evoked potentials of a similar amplitude and shape (lowermost record in *C* at a slower speed).

corresponding to the middle and caudal part of Onuf's nucleus, again in agreement with the distribution of surface potentials (Fig. 3).

Articular afferents of the posterior nerve to the knee joint also produced small field potentials at some locations but their actions were not systematically mapped.

Latency

The latencies of the largest dorsal horn field potentials of sharpest onset were 2·4–2·6 and 3·1–3·7 ms from stimuli applied to the PBST and GS nerves, respectively. When the latencies of all potentials greater than 300 μA in amplitude were measured from the time of arrival of group I volleys, the latencies of potentials evoked from PBST ranged from 1·2 to 1·9 ms (34 potentials in 10 experiments; mean 1·55 ms) and those evoked from GS ranged from 1·4 to 2·3 ms (13 potentials in 10 experiments; mean 1·87 ms). Considering that impulses in the fastest conducting group II fibres of these nerves arriving at the level of the dorsal roots are delayed with respect to those in group I fibres by 0·7–1·0 ms (Fu *et al.*

1974), the field potentials would probably be evoked with segmental delays of less than 1 ms from group II volleys. Such delays (of 0·5–0·7 ms) were in fact found in experiments in which the incoming volleys displayed a group II component (which appeared with stimuli of 2–3T and increased with stimuli of 3–5T) from which the latencies of the field potentials could be measured. However, these short latencies characterized only the more dorsally located field potentials; the latencies of field potentials in deeper parts of the grey matter were evoked at increasing latencies. Those in deeper parts of the dorsal horn were longer by 0·3–0·5 ms and those in the intermediate zone by 0·6–1·0 ms. This increase in the latencies of field potentials with depth is in keeping with the considerable slowing of conduction velocity of the deeper projecting axon collaterals of group II afferents (Fu & Schomburg, 1974; Lundberg *et al.* 1987 *a*).

Synaptic linkage

Since the central delay between the arrival of the fastest conducting group II afferents at the dorsal root entry zone and the onset of dorsal horn field potentials may be less than 1 ms, and since the central conduction time of group II afferents terminating in the dorsal horn is on average around 0·4 ms (Fu & Schomburg, 1974; Lundberg *et al.* 1987 *a*), it may be concluded that there is time for only one synaptic delay (about 0·3 ms) between the group II fibres and neurones responsible for the earliest components of the field potentials. To provide further evidence that the field potentials are evoked largely monosynaptically two further tests were performed.

Firstly, it was verified that the main part of the potentials (up to their peak) followed a train of stimuli without temporal facilitation: field potentials were faithfully evoked by trains of stimuli at frequencies of up to 600 Hz and (apart from some reduction in amplitude following the first response) without appreciable differences in the amplitude of successive potentials. Two examples of more than twenty such tests are shown in Fig. 6 *B* and *C*.

Secondly, it was verified that group II afferents do indeed project to the area within which the field potentials are evoked and that the conduction times along these fibres, when compared to the latencies of field potentials, leave time for only a single synaptic delay. Group II fibres of both ST and LG were found to be excited by stimulus pulses (mostly of less than 3 μA) applied within the same area in which dorsal horn field potentials were evoked by these nerves. Plots of the peripheral thresholds and of the overall conduction times of these fibres are shown in Fig. 7 together with the shortest latencies of dorsal horn field potentials recorded in the same experiments. If the field potentials are to be attributed to the monosynaptic actions of group II fibres, then conduction times along the fastest conducting fibres should not be more than 0·3–0·5 ms shorter than the minimal latencies of field potentials. It is evident from these plots that most of the fibres conformed to this requirement.

Two additional comments may be made with respect to the data shown in Fig. 7. (i) Fibres referred to as group I afferents were characterized by peripheral thresholds of 1·0–1·4T. Fibres referred to as group II afferents were selected using two criteria: peripheral thresholds of at least 2·0T and conduction time exceeding that of any afferents with a peripheral threshold $< 1{\cdot}5T$. Fibres with peripheral thresholds of 1·5–2·0T were excluded from analysis because they might have included both group I and group II afferents (Jack, 1978). Furthermore, since the

postsynaptic actions of group II afferents in the sacral cord were induced by stimuli $\geqslant 2T$, it is the properties of fibres excited by such stimuli that are most relevant. (ii) Conduction distances in the centrifugal direction (110–147 mm for ST and 180–195 mm for LG) were longer than those in the centripetal direction because the electrodes used to stimulate the peripheral nerves were proximal to the recording electrodes (see Methods). These differences were of the order of 10 mm for the LG nerve and of either 10 mm (short branch) or 30 mm (long branch) for the ST nerve. Some discrepancies between the conduction times of group II afferents and the latencies of field potentials are accounted for by this difference in conduction distance; 10 and 30 mm differences resulting in additional delays of 0·12–0·16 ms and 0·37–0·50 ms respectively, for fibres conducting at 80–60 m s^{-1}. This becomes a particularly significant factor for some of the ST data points in Fig.7 where all the fibres represented by the triangles were recorded from a short branch (10 mm difference) while those represented by circles and crosses include some fibres recorded from the longest branch (30 mm difference).

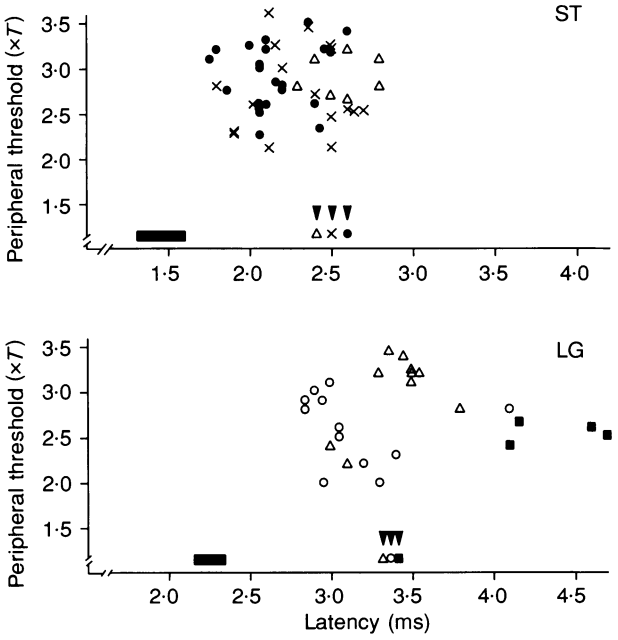

Fig. 7. Peripheral thresholds *versus* conduction times along fibres activated by intraspinal stimuli. Top panel, data for fibres in branches of the semitendinosus nerve. Bottom panel, data for fibres in one of the branches of the lateral gastrocnemius nerve. Different symbols are used for fibres recorded in separate experiments. The majority of fibres were activated by stimulus pulses of 1–4 μA applied within areas in which the largest field potentials were evoked by group II afferents of the respective nerve. The downward-pointing arrowheads above the abscissa indicate the shortest latencies of dorsal horn field potentials and the filled bars the ranges of latencies of group I fibres in the same experiments. Latencies were measured from the onset of the stimulus.

Conduction velocities

The conduction velocities of group II fibres responsible for the earliest components of the dorsal horn group II field potentials were estimated by subtracting from the latencies of these potentials: 0·3 ms for a synaptic delay, 0·3 ms for conduction time along the intraspinal axon collaterals (Fu & Schomburg, 1974; Lundberg *et al.* 1987 *a*) and 0·2 ms for the latent period of activation of these fibres by electrical stimuli applied to peripheral nerves (Jankowska & Roberts,

1972). By relating the remaining time to the conduction distances (from the peripheral nerve to the entry of the S1 dorsal root to the spinal cord) the conduction velocities of the fastest fibres evoking field potentials were calculated. These were 70, 65, 60 and 58 m s^{-1} for field potentials evoked by PBST fibres (4 experiments) and 78 and 71 m s^{-1} for field potentials evoked by GS fibres (2 experiments). These are within the range (45–92 m s^{-1}) of conduction velocities for fourty group II afferents in the nerve to ST which were activated by intraspinal stimuli applied in the dorsal horn.

Nearly one-third of the sample of fibres conducted at more than 72 m s^{-1} (which is often used to define the upper limit of conduction velocities of group II afferents) and this might appear unusually high for group II afferents. However, in comparing the data presented here with the results of other studies it should be noted that the conduction velocities were calculated after deducing 0·2 ms from the conduction time between the spinal cord and the peripheral nerves to account for the latent period of generation of action potentials. This procedure had the effect of increasing the calculated conduction velocities by about 3 m s^{-1} for the slowest conducting fibres and by 8–10 m s^{-1} for the fastest conducting fibres of our sample. When calculated without subtracting 0·2 ms, the conduction velocities of the fibres were between 42 and 82 m s^{-1} and only three exceeded 72 m s^{-1}. In addition, since all these afferents had peripheral thresholds of 2–3·5T (see Fig. 7, top panel), and those of the five fastest conducting fibres ranged between 2·5 and 3·3T they are unlikely to represent erroneously classified group I afferents (Jack, 1978).

Potentials evoked by muscle stretches

Attempts were made to find out whether the effects of electrical stimulation of group II muscle afferents could be reproduced by muscle stretches and to provide evidence for the contribution of group II muscle spindle afferents to these actions. Recordings of field potentials following muscle stretches were made in the dorsal horn at sites where electrical stimulation of group II afferents of the ST and GS nerves produced field potentials of around 700–800 μV and where there were no traces of any field potentials of group I origin. Stretches of up to 120 μm were produced with rapid rising phases (about 2 ms) in order to induce the most synchronous discharges possible. The stretches were applied to the tendons of the ST or GS muscles at initial tensions of approximately 3 N.

Figure 8 shows examples of field and cord dorsum potentials evoked by muscle stretches of 120 μm. In the records from the surface one can discern early, well-synchronized afferent volleys which, on the basis of a previous analysis (Fetz, Jankowska, Johannisson & Lipski, 1979), may be attributed to group I afferents. These were followed by very dispersed potentials which may represent impulses in slower conducting afferents and/or afferents activated less synchronously by the first stretch, or by successive oscillatory changes in muscle length. This dispersed activity was superimposed on a slower rising negative cord dorsum potential which, as for electrical stimulation, was more marked following stretches of ST than GS.

Field potentials produced by muscle stretches were much smaller than those following electrical stimulation. Their amplitudes amounted to 100–200 μV in single sweep records, and the all-or-nothing character of some of them, such as those in Fig. 8 *A*, *C* and *D*, suggested that they might be evoked by single afferent fibres. The amplitudes of averaged potentials were 20–100 μV, presumably because they were derived from irregularly or asynchroneously evoked potentials. The

small size of these potentials is not surprising since only a small proportion of muscle spindle secondaries are likely to be activated by stretches of the kind used in this study (Fetz *et al.* 1979; Jankowska, McCrea & Mackel, 1981). The results are also consistent with observations from the midlumbar segments where the

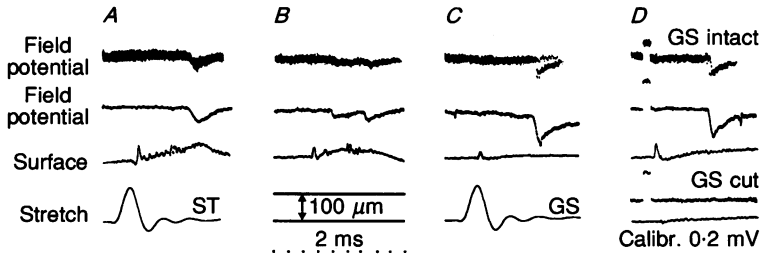

Fig. 8. Examples of field potentials evoked by rapid stretches of the ST (*A* and *B*) and GS (*C* and *D*) muscles. The records consist of three superimposed potentials (top row) and averages of sixteen potentials (second row). Afferent volleys and cord dorsum potentials evoked by the stretches are shown in the third row. The timing and amplitude of the stretches are shown in the bottom traces of *A* and *C* with the calibration in *B*. The field potentials were recorded at sites where potentials of 800 and 700 μV were evoked by electrical stimulation of the ST and GS nerves, respectively. The two sets of averaged records in *D* show effects of stretches before and after the GS nerve was transected. Calibration pulses in *D* (0·2 mV) apply to all single sweep and averaged records of field potentials.

amplitudes of stretch-evoked field potentials recorded at the same sites as group II potentials evoked by electrical stimulation did not exceed 10 % of the latter (Edgley & Jankowska, 1987 *a*).

In the absence of recognisable group II afferent volleys, the latencies of stretch-evoked field potentials have been related to the distinctly observable group I volleys. According to previous observations, impulses in group II muscle spindle afferents activated by muscle stretches of the kind used here reach the dorsal root entry zone 1·5–10 ms later than nerve impulses in group Ia afferents (Stuart, Mosher, Gerlach & Reinking, 1970; Fetz *et al.* 1979; Jankowska *et al.* 1981). Figure 8 shows that field potentials appeared as single or double responses at latencies (3–6 ms) that are in keeping with these observations. The disappearance of the stretch-evoked field potentials (Fig. 8*D*, bottom) after transection of the nerve shows that the potentials originated from afferents of the muscle that was stretched.

DISCUSSION

The results of this study demonstrate that an important relay for input from group II muscle afferents of the cat hind limb is located within a region of the spinal cord at the same rostrocaudal levels as the pudendal motor nucleus (Onuf's nucleus), i.e. caudal to the lumbosacral enlargement. Since Onuf's nucleus is most often confined to the sacral segments (see Fig. 1 and Romanes, 1951; Ueyama *et al.* 1984; Roppolo, Nadelhaft & De Groat, 1985) this relay has been referred to as the sacral group II relay. However, the location of this relay (and of Onuf's nucleus)

with respect to the spinal segments varies widely in different preparations and cannot be strictly related to particular sacral segments. Indeed in the most extreme cases, the relay was even found to extend into the caudal part of the L7 segment and this may explain why large potentials of group II origin have occasionally been seen within the lumbosacral enlargement (Fu *et al.* 1974).

Our results show that the sacral group II relay is highly specialized in that it is greatly restricted to the input from group II afferents of the knee flexor muscles semitendinosus and posterior biceps and from the ankle extensor muscle gastrocnemius. Group II afferents of other muscles proved to have either much weaker or negligible actions in the sacral segments. These include group II afferents which relay mainly in the midlumbar segments (Edgley & Jankowska, 1987 *a*) and even afferents of the closest synergists of PBST and GS (gracilis, anterior biceps, semimembranosus and plantaris, respectively; Eccles, Eccles & Lundberg, 1957; Hongo, Lundberg, Phillips & Thompson, 1984). It will be noted in this context that the effects of group II afferents of the posterior biceps–semitendinosus were only rarely seen in the midlumbar segments (Edgley & Jankowska, 1987 *a*, *b*) and in the caudal lumbar segments (Fu *et al.* 1974). These results therefore provide further evidence for a topographic separation of neurones relaying information related to the lengths of various muscles.

The receptor origin of the group II fibres

In most muscle nerves, afferents classified as group II afferents consist of those which originate from secondary endings of muscle spindles together with a variable number of afferents of non-spindle origin. We nevertheless propose that muscle spindle secondaries are partly, if not primarily, responsible for the effects induced by electrically activating group II afferents of the PBST and GS nerves in the sacral segments. The reasons for this proposal are the following: (i) the ST and MG nerves are amongst those muscle nerves in which group II afferents are most homogenous with regard to their receptor origin. Both anatomical evidence relating the number of group II afferents to the number of muscle spindles (Hunt, 1954; Boyd & Davey, 1968) and electrophysiological evidence from recordings from afferents identified with regard to receptor origin by adequate activation (Jack, 1978; Rymer, Houk & Crago, 1979), suggest that most group II afferents in these nerves originate from muscle spindles; (ii) studies of non-spindle group II afferents in the MG nerve show them to conduct mainly within the lower range of group II conduction velocities (Rymer *et al.* 1979; Cleland, Hayward & Rymer, 1990) while evidence from the present study shows that field potentials evoked within the sacral segments are mediated by the fastest conducting fraction of group II afferents; (iii) the peripheral thresholds and conduction velocities of fibres activated from within the same area of the sacral cord in which field potentials of group II origin were recorded are in keeping with those of identified muscle spindle secondaries of the ST and MG nerves (Jack, 1978); (iv) group II muscle spindle afferents (of GS) identified by adequate activation of their receptors have been found, using both intraspinal stimulation (Fu & Schomburg, 1974) and intra-axonal staining with horseradish peroxidase (for references see Introduction), to terminate in the L7 segment in regions equivalent to those in which field potentials are

induced by group II afferents in the sacral segments; (vi) in this study muscle stretches evoked field potentials in the sacral segments at the same sites at which they were induced by electrical stimuli. Similar observations have been made in the midlumbar segments (Edgley & Jankowska, 1987*a*, 1988) where field potentials have also been shown to appear following activation of muscle spindle afferents by fusimotor neurones (Harrison, Jami & Jankowska, 1988; see Hunt, 1952). On this evidence we therefore conclude that group II secondaries must contribute to the actions of group II afferents within the sacral segments though non-spindle group II afferents may also be involved.

Possible functional advantages of the topographical separation of relays of group II afferents of different nerves

Taken together, observations reported in this and previous studies (Edgley & Jankowska, 1987*a*,*b*) demonstrate that neurones relaying information from group II muscle afferents, in particular those located within the dorsal horn, are to a great extent concentrated outside the lumbosacral enlargement, in contrast to neurones in reflex pathways from group Ia muscle spindle and group Ib tendon organ afferents which are located mainly within the enlargement. All previously investigated interneuronal populations, including those of the midlumbar segments, consist of funicular neurones which have their target cells spread over several segments. Their location does not therefore need to be strategically situated close to the motoneurones, or other neurones which they contact. The axonal projections of interneurones located in the sacral segments are under investigation, but since these might also be funicular neurones there are no *a priori* reasons to expect that their location necessarily bears any functional relationship to groups of neurones in the near vicinity. Nevertheless, the close anatomical relationship between the sacral group II relay area, pudendal motoneurones and motoneurones of toe, tail, and levator ani muscles (see Romanes, 1951; Sato *et al.* 1978) might be advantageous if these motoneurones are among the targets of interneurones of the sacral relay area. However, although PSPs have been recorded in motoneurones of the external anal sphincter muscle following stimulation of the PBST and/or GS nerves, only oligosynaptically evoked actions have been reported (Fedirchuk, Hochman & Shefchyk, 1992).

A more essential advantage of the topographical separation of group II relay neurones in the midlumbar and sacral segments might be that it provides the opportunity for the integration of information on the length of various muscles with appropriate information from other types of receptors. For example, it may be of functional advantage that information from receptors in certain muscles be processed together with cutaneous sensory input related to a particular area of skin, such as that overlying the relevant muscles. The information to hand shows for instance that the midlumbar interneurones are more effectively excited by afferents of the saphenus nerve (from skin overlying Q and Sart muscles) than the sacral interneurones, while the latter are more effectively excited by afferents of the pudendal and cutaneous femoris nerves (from skin overlying the ST muscle; E. Jankowska & J.S. Riddell, in preparation, and J.S. Riddell & E. Jankowska, in preparation). It may also be of advantage, if these neurones are involved in

mediating different reflex actions and are under the control of different neuronal systems, that these neuronal systems operate preferentially within different spinal segments.

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