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CUTANEOUS EXCITATORY AND INHIBITORY INPUT TO NEURONES OF THE POSTSYNAPTIC DORSAL COLUMN SYSTEM IN THE CAT

BY R. NOBLE* AND J. S. RIDDELL†

From the Department of Preclinical Veterinary Sciences, University of Edinburgh, Summerhall, Edinburgh EH9 1QH

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SUMMARY

1. In chloralose-anaesthetized cats single-unit microelectrode recordings were made from axons in the dorsal columns, at the lumbar level, identified as belonging to the postsynaptic dorsal column (PSDC) system.

2. Excitatory and inhibitory receptive field arrangements of a sample of seventy-five PSDC neurones were examined in detail using natural cutaneous stimuli.

3. The sample was characterized by a high degree of convergent input: 80% of units were activated by both light tactile and noxious mechanical stimuli and more than half of those examined were excited by noxious radiant heat. In addition, three-quarters of the units had inhibitory receptive fields on the ipsilateral limb.

4. Twenty-three units (27%) were influenced by input from areas of both hairy and glabrous skin covering the foot and distal limb. Neurones in this group had complex receptive fields, many of which occupied several discontinuous areas of skin. Background and evoked activity of these units could frequently be inhibited by light tactile and/or noxious stimuli. Their inhibitory receptive fields occupied small areas of skin overlapping or adjacent to excitatory fields.

5. Fifty-two units (73%) had receptive fields restricted to areas of hairy skin on the thigh and upper hindlimb. Half the units in this group had coextensive low- and high-threshold excitatory areas but about one-third had a concentric receptive field organization; a high-threshold excitatory component extending beyond, or around, a central low-threshold area. The discharge of these units could be inhibited only by light tactile stimuli. Their inhibitory receptive fields covered extensive areas of skin, sometimes completely surrounding the excitatory field.

6. The complex receptive field arrangements observed for neurones of the postsynaptic dorsal column system are discussed in relation to previous observations on dorsal horn neurones of other ascending tracts.

* Present address: Department of Physiology and Biochemistry, University of Reading, Whiteknights, P.O. Box 228, Reading RG6 2AJ.

† Present address and address for correspondence: Department of Physiology, University College London, Gower Street, London WC1E 6BT.

INTRODUCTION

Neurones of the postsynaptic dorsal column (PSDC) system form an ascending spinal pathway providing somaesthetic input to the dorsal column nuclei (see Brown, 1981, for review). Previous investigators of the receptive field organization of PSDC neurones, recorded in pentobarbitone-anaesthetized cats, have reported similarities between these neurones and cells of the spinocervical tract (SCT) (Uddenberg, 1968; Angaut-Petit, 1975; Lu, Bennett, Nishikawa, Hoffert & Dubner, 1983). However, recent work has shown that the PSDC and SCT systems arise, at least in substantial part, from separate populations of neurones in the dorsal horn (Brown, Noble & Riddell, 1986). Furthermore, studies of the morphology (Brown, Rose & Snow, 1977; Brown & Fyffe, 1981; Enevoldson, 1982) and ultrastructure of neurones of the two systems have revealed important differences between them. PSDC neurones are contacted by boutons which may participate in axo-axonic contacts, triadic arrangements and glomerular complexes (Maxwell, Koerber & Bannatyne, 1985; (Bannatyne, Maxwell & Brown, 1987), suggesting that both their course and fine fibre inputs are subject to presynaptic modulatory influences. In contrast, neurones of the SCT have a simple ultrastructural organization and their direct afferent input appears largely free of presynaptic control (Maxwell, Fyffe & Brown, 1982, 1984). These observations suggest that afferent input to these two somatosensory pathways may be processed in different ways and this is likely to be reflected in different response properties and receptive field organizations for PSDC and SCT neurones.

For PSDC neurones recorded in the chloralose-anaesthetized cat, some differences have already been noted (Brown & Fyffe, 1981; Brown, Brown, Fyffe & Pubols, 1983); but these studies involved relatively small samples of units, most of which had distally located receptive fields on the foot or toes. In the experiments to be reported in the present paper we have investigated the receptive field arrangements of a larger sample of identified PSDC units including those with receptive fields on proximal regions of the limb.

Some of the results presented here have appeared in a preliminary report (Noble & Riddell, 1984).

METHODS

Preparation

Experiments were performed on cats (2·1–2·7 kg body weight) anaesthetized with chloralose (70 mg/kg) after induction with halothane in an oxygen and nitrous oxide mixture. The adequacy of anaesthesia was assessed by frequent inspection of pupil diameter and of a continuous arterial blood pressure recording. Supplementary doses of chloralose (50–100 mg) were given as required. The cats were intermittently paralysed with gallamine triethiodide and artificially respired. End-tidal CO_2 was maintained at about 4% and rectal temperature at 38 °C. Electrophysiological recordings were discontinued if the mean blood pressure fell below 80 mmHg.

Electrical stimulating and recording procedures

A diagrammatic representation of the preparation on which are indicated the positions of stimulating and recording electrodes is shown in Fig. 1. The spinal cord was exposed by laminectomies performed at C1–C4 and L3–L7 inclusive. The dorsal columns were sectioned at C1–C2 using watchmakers' forceps, the lesion being extended gradually until the initial negative component of a cord dorsum potential recorded at L7, in response to stimulation of the dorsal columns above the site of transection, was abolished (see Brown *et al.* 1986). Bipolar silver-ball

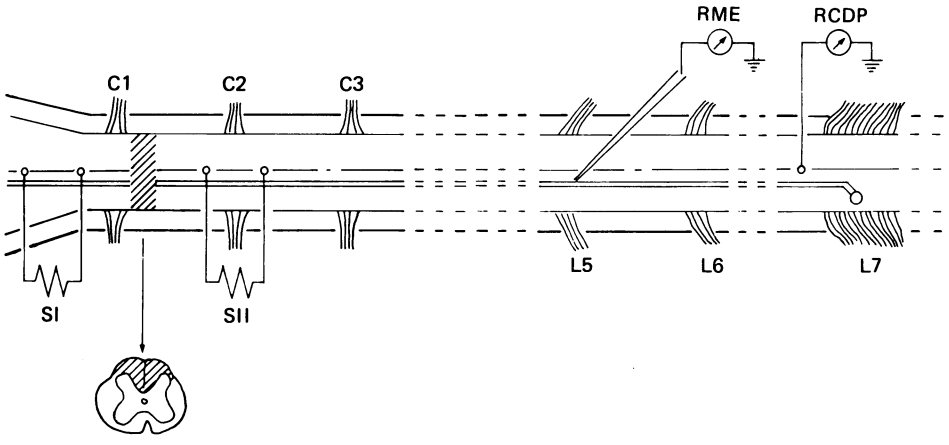

Fig. 1. Diagrammatic representation of the experimental arrangement. The drawing represents a dorsal view of the spinal cord at the cervical (C1–C3) and lumbar (L5–L7) enlargements. SI and SII represent stimulation sites on the dorsal columns above (C1) and below (C2) a lesion of the dorsal columns at C1–C2 (indicated by hatching). RME, recording micro-electrode; RCDP, cord dorsum recording electrode.

electrodes were used to apply search stimuli (3 V, 250 μA, 0·1 ms once every 600 ms) to the dorsal columns at C2 below the lesion, and extracellular recordings made from axons in the dorsal columns at L4–L6 using glass capillary microelectrodes containing 4 M-NaCl with impedances of 15–20 MΩ.

Identification criteria

Postsynaptic dorsal column fibres were differentiated from primary afferent fibres by a convergence of cutaneous afferent input and/or by an irregular, bursting background activity. All postsynaptic units were shown to project at least to upper cervical levels by antidromic activation from an electrode on the dorsal columns at C2–C3. Antidromic impulses were identified by both collision with orthodromic impulses and by their ability to follow trains of stimuli of at least 500 Hz. The dorsal columns are also known to contain fibres descending the spinal cord (Dart, 1971; Enevoldson & Gordon, 1984). Contamination of the sample of PSDC axons was avoided by the lesion of the dorsal columns which prevented postsynaptic activation of descending fibres.

Cutaneous stimuli

The hair on the hindlimbs was clipped and the cutaneous receptive fields of identified PSDC units investigated using both light tactile and noxious stimuli. Light tactile stimuli were applied using a variety of blunt hand-held probes, air jets and a motorized brush. In addition, tuning forks were employed to apply vibratory stimuli.

Noxious stimuli (i.e. stimuli painful to the investigator) were applied in both mechanical and thermal forms. A maintained noxious pinch was produced by a clip applied to a skin fold, while noxious radiant heating was produced by a halogen lamp with an integral focusing reflector (Beck, Handwerker & Zimmerman, 1974; Fitzgerald & Lynn, 1977). The radiant heating produced a ramp increase in skin surface temperature to a maximum of between 50 and 55 °C over a period of about 8 s, at which point the stimulus was terminated. Similar paradigms have been shown to be effective in exciting thermal nociceptive afferent fibres (Kumazawa & Perl, 1977; Georgopoulos, 1976) but do not produce visible signs of injury, provided that the heating is not repeatedly applied at the same skin location.

Excitatory and inhibitory receptive fields were investigated in detail and were mapped on photographs of the cat's hindlimb. All responses were recorded on magnetic tape and analysed on- and off-line. Impulse frequency histograms were prepared using a computer (Cromenco Systems III).

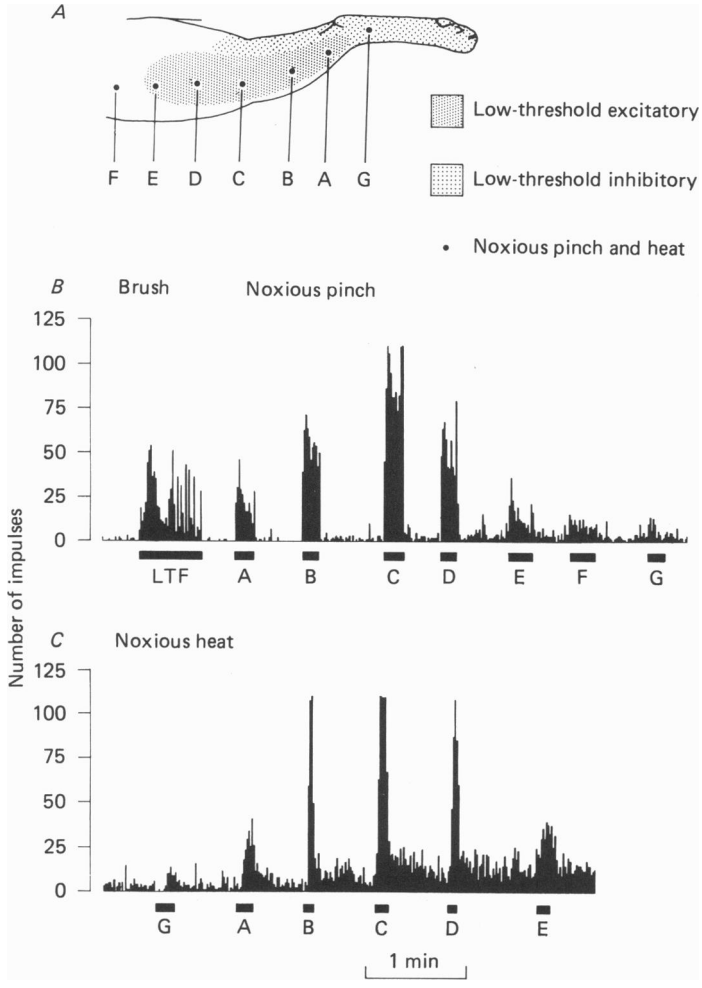

Fig. 2. Typical excitatory responses of a PSDC neurone to cutaneous mechanical and thermal stimuli. *A*, outline of a cat's hindlimb on which are indicated the low-threshold excitatory and inhibitory receptive field components of a PSDC neurone. The locations labelled A–G represent the positions at which noxious mechanical and thermal stimuli were applied. *B*, impulse frequency histogram in which the number of impulses occurring in 1 s bins is plotted against time. The histogram shows responses to brushing the low-threshold excitatory field (LTF) and to noxious pinch applied to each of the skin positions A–G. Stimulus durations are indicated by filled bars. *C*, responses of the same unit to noxious radiant heat. Note the gradient of sensitivity within the high-threshold excitatory field.

RESULTS

Detailed investigations were made of the response properties and receptive fields of seventy-five identified PSDC neurones all of which had a background discharge. Areas of skin from which light brushing or tapping evoked responses were designated low-threshold fields. Pinch-responsive fields were initially investigated using two clips of different force, one judged to be innocuous the other noxious. However, all of those units (thirty-two) which responded with a slowly adapting discharge to a

noxious pinch, were also activated by innocuous pinch and it was not possible to differentiate with any certainty between input from low- and high-threshold receptors. Therefore, in subsequent experiments, areas of skin from which a sustained noxious pinch evoked a slowly adapting discharge were tentatively designated high-threshold fields. About half of the sample of units were also investigated for their response to noxious radiant heat.

TABLE 1. Summary of the convergence of cutaneous input to a sample of seventy-five postsynaptic dorsal column neurones

Excitatory receptive field type	Number of units (%)	Number with inhibitory fields (%)	Receptive field location		
			Hairy skin	Glabrous skin	Hairy and glabrous skin
Low threshold	8 (11)	7 —	2	1	5
High threshold	1 (1)	1 —	1	0	0
Low and high threshold	66 (88)	48 —	49	2	15
Total	75 (100)	56 (75)	52	3	20

Convergence of input

Convergence of cutaneous input was a major feature of the PSDC neurones investigated. Sixty-six of the seventy-five units (88%) received both low- and high-threshold excitatory input from cutaneous mechanoreceptors while more than half of the units tested (22/39) were also excited by noxious radiant heat. Of the remaining nine units in the sample, eight responded only in a rapidly adapting fashion to light tactile stimuli and one unit could be excited only by stimuli of a noxious intensity. Typical examples of excitatory responses to these mechanical and thermal cutaneous stimuli are shown in Fig. 2. In addition to convergent excitatory input, fifty-six of the seventy-five units (75%), were found to have inhibitory fields on the ipsilateral hindlimb. Although detailed observations were mainly confined to skin of the ipsilateral limb occasional searches of the contralateral limb failed to detect either excitatory or inhibitory input. Fifty-two units had receptive fields restricted to hairy skin while those of two units were confined to the glabrous skin of the toe and foot pads. Twenty units (27%), however, received input (excitatory and/or inhibitory) from receptors in both hairy and glabrous skin. The convergent properties of PSDC neurones are summarized in Table 1.

In addition to the seventy-five units described above, a further small number (nine) were recorded which behaved as if excited exclusively by Pacinian afferent fibres. These units had a background activity which, though irregular, lacked the bursts of impulses characteristic of clearly identified PSDC units (see below). Since these units could not conclusively be shown to be postsynaptic they are not considered further in the present paper.

Receptive field organization

The main aim of the present study was to examine the cutaneous receptive field organization of PSDC neurones recorded under chloralose anaesthesia. Previous reports have largely been confined to units with receptive fields located on the distal

regions of the limb, most of which included areas of glabrous skin (Brown & Fyffe, 1981; Brown *et al.* 1983). The present study has extended these observations to include neurones with receptive fields on more proximal regions of the hindlimb and confined to the hairy skin. These observations have revealed distinct differences between the two groups of units each of which are described below.

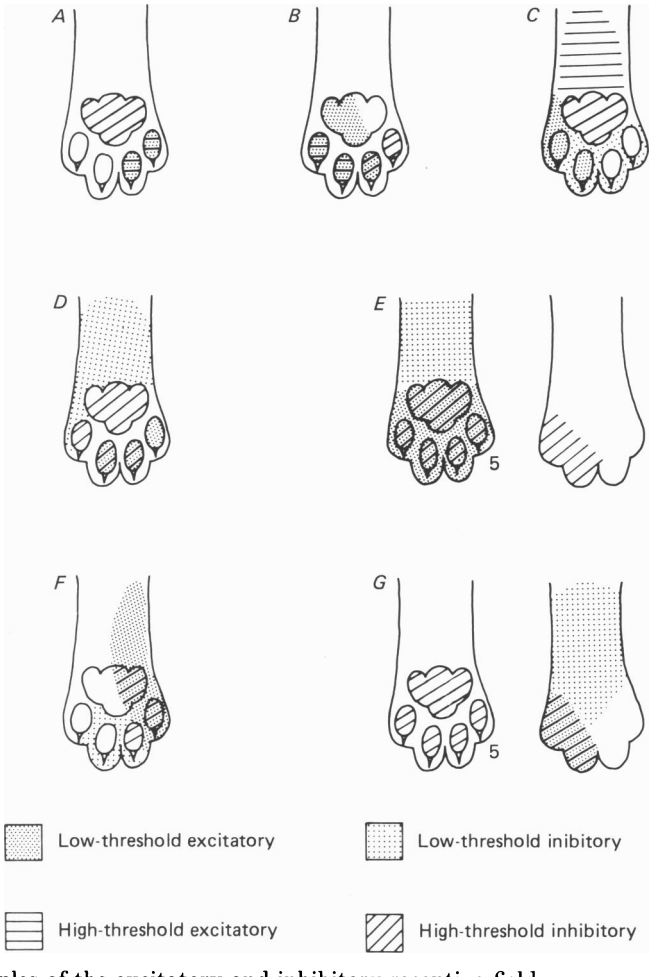

Fig. 3. Examples of the excitatory and inhibitory receptive field arrangements of PSDC neurones receiving input from receptors in glabrous skin (*A* and *B*) or both hairy and glabrous skin (*C–G*). Further details are given in the text.

Glabrous skin units

Twenty-three units from the present sample (27%) had receptive fields on the distal hindlimb which included areas of the glabrous skin of the toe or foot pads. It should be emphasized, however, that most (twenty) of these units also received input from adjacent areas of hairy skin. Figure 3 shows examples of the types of excitatory and inhibitory receptive field arrangements observed for units of this group.

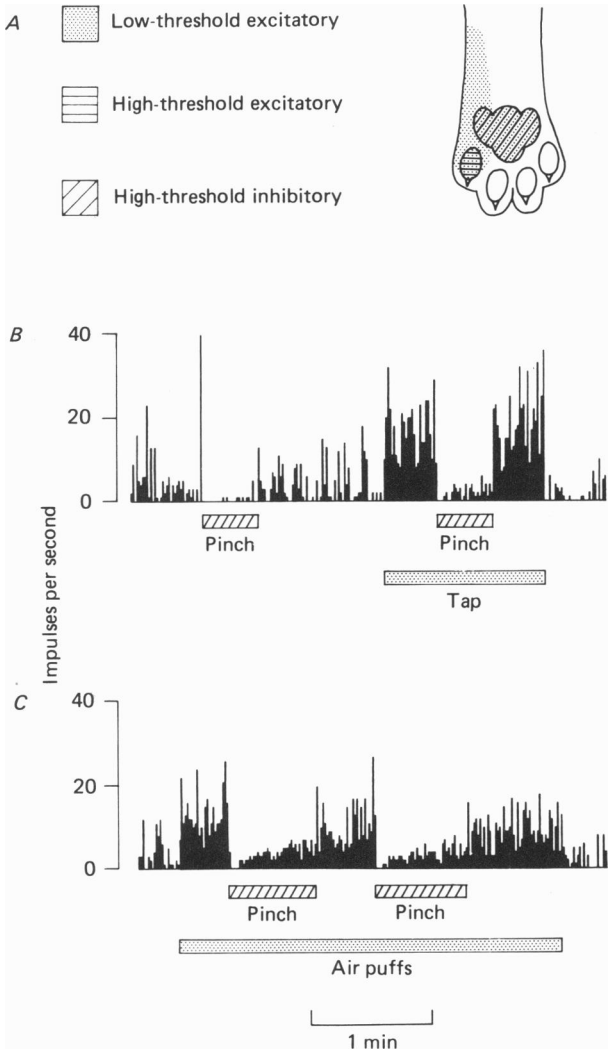

Fig. 4. Examples of inhibition evoked in a PSDC neurone by noxious pinch. *A*, outline of a cat's hind paw on which are shown the receptive field components of a PSDC neurone. *B*, impulse frequency histogram (1 s bins) of a period of recording from the unit shown in *A*. Noxious pinch applied to the central pad (hatched bars) produced inhibition of both background discharge and activity evoked by tapping a toe pad (shaded bar). *C*, noxious pinch applied to the central pad (hatched bars) produced inhibition of activity evoked by an air jet (once evey 1·5 s, shaded bar) applied to the hairy skin of the low-threshold excitatory field. Note that some activity recovers as the response to the noxious stimulus adapts.

Excitatory receptive fields. All twenty-three units of this group could be activated by light tactile stimuli and seventeen responded with a slowly adapting discharge to a maintained pinch. Five of twelve units tested were in addition excited by noxious radiant heat (six were inhibited, see below).

The majority of units was particularly sensitive to gentle stimuli applied to the

glabrous skin of the toe or foot pads and could also be activated at a distance by tapping the recording frame or table. These responses presumably reflect input from rapidly adapting mechanoreceptors in glabrous skin since units were generally unresponsive to a maintained pinch applied to all, or part, of the tap-responsive area. Despite their extreme sensitivity, none of those tested (eight) followed the vibrations of a tuning fork (384 Hz) for more than a few cycles.

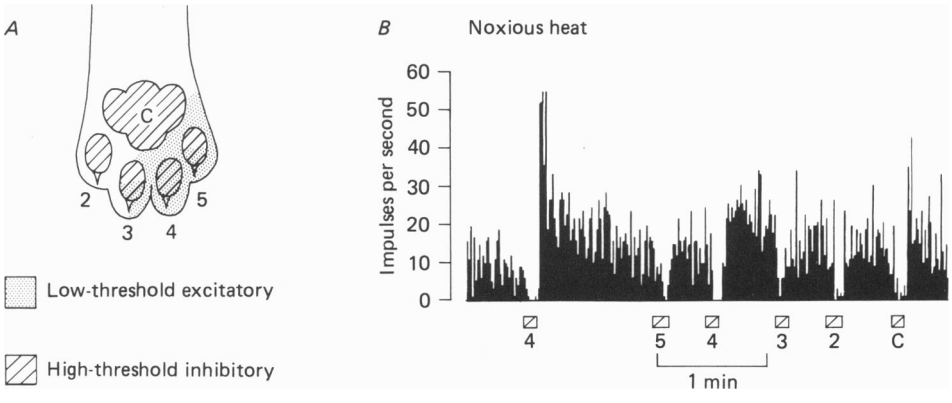

Fig. 5. Examples of inhibition evoked in a PSDC neurone by noxious radiant heat. *A*, outline of a cat's hind paw on which are shown the receptive field components of a PSDC neurone. *B*, impulse frequency histogram (1 s bins) showing the inhibition of background activity produced by noxious radiant heat applied to the glabrous skin of each of the toe and foot pads. Note that a rebound excitation followed the inhibition evoked from toe pad 4.

A common feature of units in this group was that low- and high-threshold excitatory field components were discontinuous; typically these occupied a number of sensitive pads which were separated by an area of hairy skin where stimuli were ineffective (Fig. 3*A*, *B*, *C* and *D*). A smaller proportion of cells had continuous excitatory fields composed of both glabrous and adjacent hairy skin (Fig. 3*E* and *F*). An equally common observation was that low- and high-threshold excitatory field components occupied, either entirely or in part, separate regions of skin (Fig. 3*B* and *C*).

Inhibitory receptive fields. Inhibitory input was detected for nineteen of the twenty-three cells of this group. Fourteen units were inhibited by light tactile stimuli and thirteen by maintained pinch; eight units being inhibited by both forms of stimuli. In addition, six of those units inhibited by noxious pinch (all of those tested) were also inhibited by noxious radiant heat. Examples of the actions of this inhibition on both background and evoked neuronal discharges are shown in Figs 4 and 5. Inhibition evoked by noxious pinch was most effective at the onset of the stimulus with partial and gradual recovery of activity occurring throughout the duration of the stimulus (Fig. 4*C*). The inhibition did not outlast withdrawal of the stimulus and repetition of stimuli evoked similar responses.

Low-threshold inhibitory components were located either on small areas of hairy skin around the pads (Fig. 3*C* and *F*) or on more extensive regions of the ventral or dorsum aspects of the foot (Fig. 3*D*, *E* and *G*); but never involved glabrous skin. In contrast, high-threshold inhibitory components were always located on glabrous skin

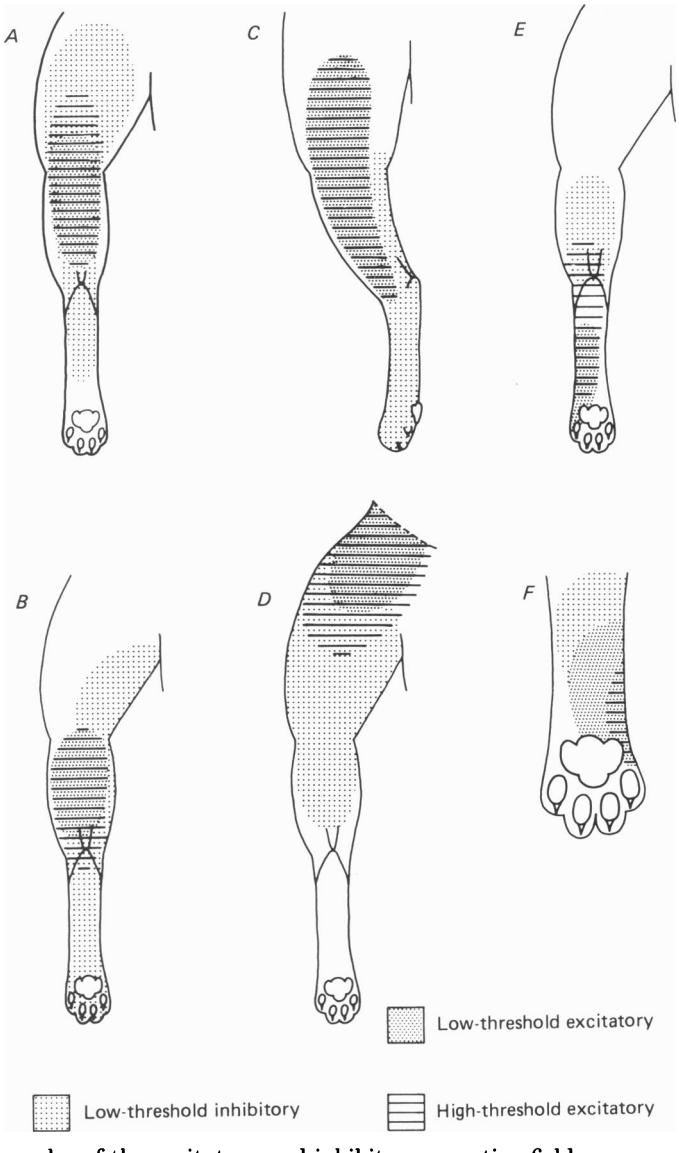

Fig. 6. Examples of the excitatory and inhibitory receptive field arrangements of PSDC neurones with receptive fields restricted to the hairy skin. Further details are given in the text.

(Fig. 3*A–G*) and were often discontinuous, involving a number of the pads but not the hairy skin between them. Frequently they were located on the same pads from which the unit could be activated by gentle tapping.

Hairy skin units

Fifty-two of the seventy-five PSDC neurones forming the present sample (73%) had excitatory and, where present, inhibitory receptive fields restricted to hairy skin on the thigh and proximal hindlimb. Figure 6 shows examples of the excitatory and inhibitory receptive field arrangements of neurones of this group.

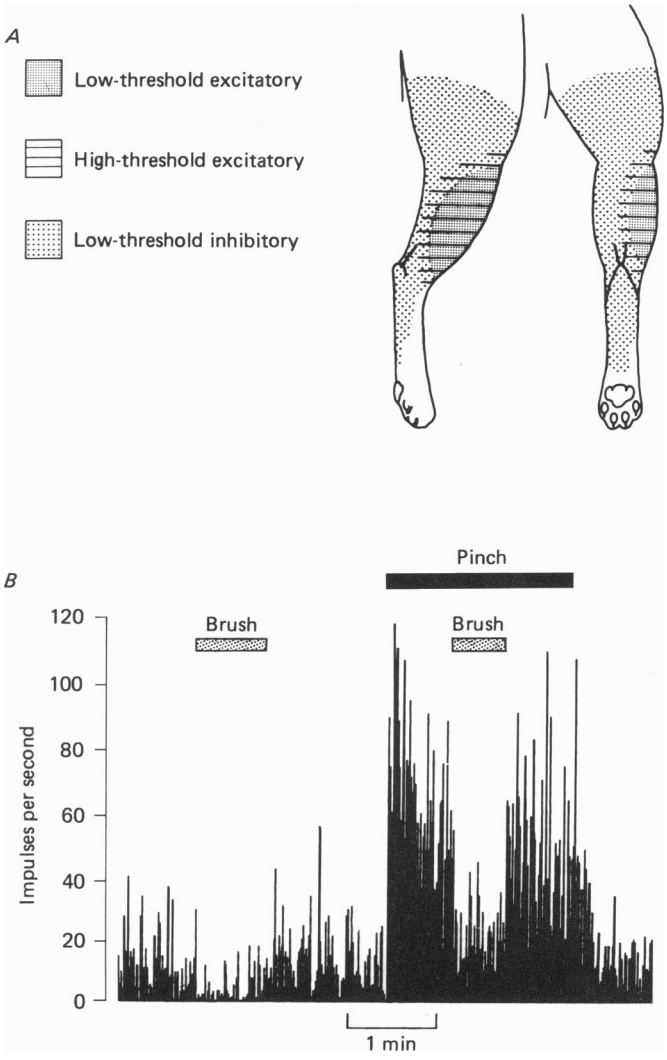

Fig. 7. Example of the inhibition evoked in a PSDC neurone by light tactile stimuli. *A*, outline of a cat's hindlimb on which are shown the receptive field components of a PSDC unit. Note that the inhibitory area covers an extensive area of skin completely surrounding the excitatory field. *B*, impulse frequency histogram (1 s bins) of a period of recording from the unit shown in *A*. Light brushing of the inhibitory field (stippled bar) reduced both the background discharge and activity evoked by pinching the excitatory field (filled bar).

Excitatory receptive fields. All but one of the units of this group could be activated by light brushing of hairy skin. Low-threshold excitatory field components had diffuse, indistinct boundaries particularly where these bordered upon low-threshold inhibitory areas (see below). In addition, fifty of the fifty-two units responded with a slowly adapting discharge to a maintained noxious pinch and of twenty-seven units tested, seventeen were excited by noxious radiant heat. Responses to noxious

mechanical and thermal stimuli were generally graded within the high-threshold excitatory field, being most vigorous near the centre and decreasing towards the edge (see Fig. 2).

The low- and high-threshold excitatory components of about half (twenty-seven) of the units covered coextensive areas of hairy skin (Fig. 6*C*). However, about one-third (sixteen) of the units in this group had high-threshold excitatory components that overlapped the low-threshold area and extended beyond it either proximally (i.e. towards the trunk; Fig. 6*A* and *E*), distally (i.e. towards the foot; Fig. 6*B*) or concentrically (Figs 6*D* and 7*A*). A small number of units (seven) had high-threshold excitatory components that were more restricted, and lay within the low-threshold area (Fig. 6*F*).

Inhibitory receptive fields. In contrast to PSDC neurones influenced by input from glabrous skin, units with receptive fields restricted to hairy skin could only be inhibited by light tactile stimuli (Fig. 7). Low-threshold inhibitory fields were detected for thirty-seven of the fifty-two units and generally covered large areas of skin on the ipsilateral limb overlapping, or adjacent to, the excitatory field (Fig. 6). The inhibitory areas of about one-third of the units virtually surrounded the excitatory field (Figs 6*A*, *B* and 7*A*) and inhibition could often be evoked from within high-threshold excitatory fields where these extended beyond their low-threshold components (Fig. 7*A*, *B*, *D* and *E*).

General properties of the whole sample

Stability of receptive fields

PSDC axons for which thorough receptive field examinations were completed were frequently recorded for periods of an hour or more. During the course of these investigations the borders of receptive field components were often examined on a number of occasions. Whilst, as previously noted, the edges of light tactile components were often indistinct, unequivocal changes in receptive field borders could not be detected.

Background activity

All seventy-five of the identified PSDC neurones investigated had a background activity when first recorded, even before any manipulation of the receptive field had occurred. The discharge pattern typically consisted of high-frequency (> 800 Hz) bursts of activity (4–12 impulses) interspersed with single, or less commonly pairs, of action potentials. The average levels of background activity recorded from nineteen units over periods of between 1 and 2 min ranged between 0·9 and 22·6 impulses/s.

Conduction velocities

Antidromic conduction velocities were measured for a total of 111 identified PSDC units, 75 of which were subsequently investigated in detail. Conduction velocities, measured between the stimulating electrode on the cervical dorsal columns and the lumbar recording site, ranged between 14 and 69 m s^{-1} (38·0 $\pm$ 12·1; mean $\pm$ S.D.) (Fig. 8*A*).

Within the sample those units with receptive fields including glabrous skin of the toe and foot pads appeared on average to have higher conduction velocities than

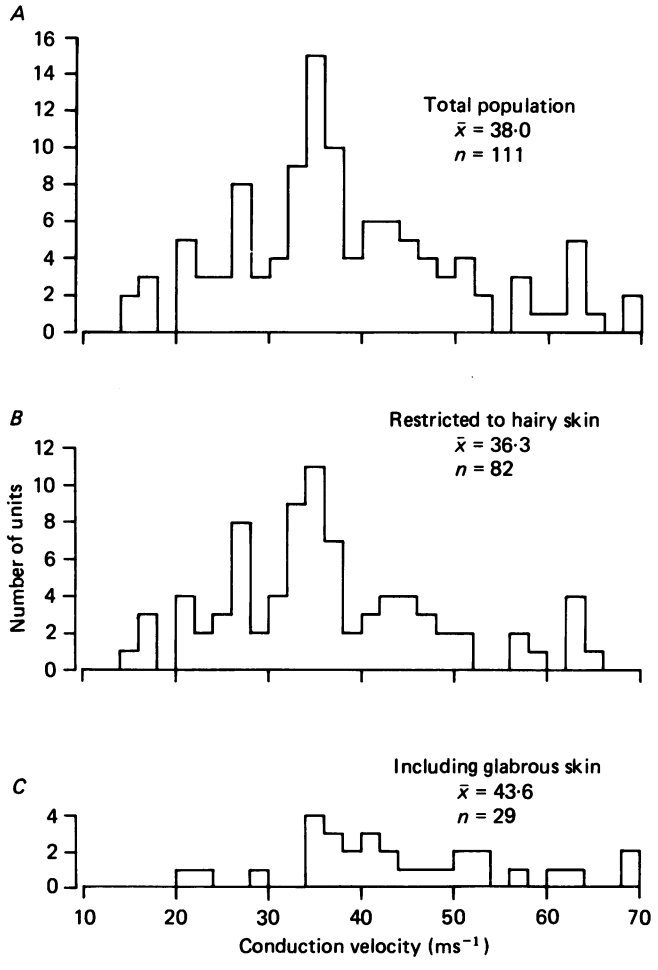

Fig. 8. Frequency histograms of the conduction velocities of PSDC axons measured between a stimulating electrode on the cervical dorsal columns and the lumbar recording site. *A*, conduction velocities of total sample. *B*, conduction velocities of units with receptive fields restricted to hairy skin. *C*, conduction velocities of units with receptive fields including glabrous skin. $\bar{x}$ = mean conduction velocity, n = number of units.

units with receptive fields restricted to hairy skin (Fig. 8*B* and *C*). This observation was investigated using single-factor analysis of variance and the difference found to be highly significant ($P < 0{\cdot}001$).

DISCUSSION

Previous reports of the receptive field arrangements of PSDC neurones recorded in pentobarbitone-anaesthetized animals have stressed their similarity with neurones of the SCT (Uddenberg, 1968; Angaut-Petit, 1975; Lu *et al.* 1983), while experiments on chloralose-anaesthetized animals suggest a considerably more complex receptive field organization (Brown & Fyffe, 1981; Brown *et al.* 1983). The present observations confirm that the majority of PSDC neurones, at least in the chloralose-anaesthetized preparation, have complex receptive fields which differ in their organization from

those of identified neurones of the SCT (Hongo, Jankowska & Lundberg, 1968; Brown & Franz, 1969; Brown, Koerber & Noble, 1987).

The great majority (88%) of the sample of PSDC neurones examined received a convergence of excitatory input from both low- and high-threshold mechanoreceptors. Eleven per cent of the sample received only low-threshold rapidly adapting excitatory input and only one unit required a stimulus of a noxious intensity for activation. These observations are in broad agreement with those of Angaut-Petit (1975) for a large population of PSDC neurones recorded from the gracile funiculus in the pentobarbitone-anaesthetized cat.

It has been reported (Kamogawa & Bennett, 1986) that PSDC neurones are relatively unresponsive to noxious thermal stimuli, being excited only after sensitization by prolonged (30 s) and repeated (three to seven trials) heating to between 50 and 56 °C. However, the present results, in agreement with those of Angaut-Petit (1975), have shown that about 50% of PSDC neurones may be excited by noxious radiant heat. Furthermore, in the present preparation, vigorous responses could be elicited without prior sensitization (Fig. 2). There are no obvious reasons for this discrepancy; both Angaut-Petit (1975) and Kamogawa & Bennett (1986) used pentobarbitone-anaesthetized preparations and both used a contact thermode to provide the thermal stimulus. Furthermore, the rates of rise and ranges of temperatures employed by Kamogawa & Bennett (1986) are similar to those used in the present experiments.

The vigorous responses of these neurones to noxious mechanical and thermal stimuli observed in the present study are consistent with reports that the dendrites of PSDC neurones frequently enter lamina II and even I (Brown & Fyffe, 1981) and that these dendrites may participate in glomerular synaptic complexes (Bannatyne, Brown, Fyffe & Maxwell, 1982; Bannatyne *et al.* 1987), the central terminals of which are thought to originate from Aδ or C primary afferent fibres (Gobel, Falls & Humphrey, 1981; Rethelyi, Light & Perl, 1982; Kniyihar-Csillik, Csillik & Rakic, 1982). These observations suggest that PSDC neurones may receive a direct input from nociceptive afferent fibres.

The present study has been predominantly concerned with the receptive field organization of PSDC neurones. Previous studies of these neurones in the pentobarbitone-anaesthetized cat (Uddenberg, 1968; Angaut-Petit, 1975; Lu *et al.* 1983) have reported that the low-threshold mechanoreceptive and nociceptive components of their excitatory fields were located on coextensive areas of skin, as is the case for cells of the SCT (Brown & Franz, 1969). However, in the present sample from chloralose-anaesthetized cats, low- and high-threshold excitatory receptive field components were commonly located on separate, or only partially overlapping, areas of skin. About one-third of the sample of units with receptive fields restricted to the hairy skin had excitatory fields composed of a central low-threshold area superimposed on a larger area responsive to noxious stimuli. This concentric type of organization has been described previously for neurones of the spinothalamic tract in the monkey (Willis, Trevino, Coulter & Maunz, 1974; Price, Hayes, Ruda & Dubner, 1978) and is also characteristic of certain unidentified dorsal horn neurones in the cat (Taub & Bishop, 1965; Wall, 1967) referred to by Wall as 'lamina V type' cells (Wall, 1969; Hillman & Wall, 1969; Devor & Wall, 1976).

PSDC neurones with distally located receptive fields often received input from

glabrous skin of the toe or foot pads. A characteristic feature of these units was that their excitatory components were often composed of several discontinuous areas of skin. Some of these areas contained both low- and high-threshold excitatory components but equally as often the two components were located on entirely separate areas of skin. While a small minority of units with spatially separate excitatory fields has been previously reported among samples of unidentified dorsal horn neurones (Devor & Wall, 1976; Pubols & Goldberger, 1980; Brenowitz & Pubols, 1981) these have always been located on the most proximal areas of the limb. Indeed, apart from previous studies of this system in the chloralose-anaesthetized cat (Brown & Fyffe, 1981; Brown *et al.* 1983), there are no reports of dorsal horn neurones with complex receptive fields of the type that have been observed for PSDC units with input from glabrous skin.

Several previous studies of PSDC neurones in the pentobarbitone-anaesthetized cat have failed to detect inhibitory input (Uddenberg, 1968; Angaut-Petit, 1975; Lu *et al.* 1983), but inhibitory fields have been reported in about half of a sample of PSDC neurones recorded in the chloralose-anaesthetized cat (Brown *et al.* 1983). The present results confirm that a large proportion (75%) of PSDC neurones, at least in the chloralose-anaesthetized cat, have inhibitory receptive fields on the ipsilateral limb. Previous observations have been extended by examining the inhibitory input to PSDC neurones with proximally located receptive fields. In contrast to neurones with input from glabrous skin, which may frequently be inhibited by both light tactile and nociceptive input, units with receptive fields confined to hairy skin could only be inhibited by light tactile stimuli. These low-threshold inhibitory regions covered extensive areas of skin adjacent to and, in some cases, virtually surrounding the excitatory field.

'Inhibitory surrounds' have been reported previously for unidentified neurones in the dorsal horn and are a characteristic feature of the 'lamina V type' neurones described by Wall (1967) and Hillman & Wall (1969). Surround inhibition has also been described for neurones at other stages in the dorsal column system: in the dorsal column nuclei (Gordon & Jukes, 1964; Andersen, Etholm & Gordon, 1970; Bystrzycka, Nail & Rowe, 1977; Aoki, 1981); the thalamus (Poggio & Mountcastle, 1963; Gordon & Manson, 1967; Baker, 1971; Janig, Spencer & Younkin, 1979) and in the somatosensory cortex (Mountcastle & Powell, 1959; Baker, Tyner & Towe, 1971; Laskin & Spencer, 1979). It has generally been considered to provide a mechanism for improving spatial discrimination of tactile stimuli (Mountcastle & Powell, 1959; Gordon & Paine, 1960; Andersson, 1962).

Surround inhibitory fields have not been observed for other identified dorsal horn neurones: cells of the SCT in the cat and spinothalamic tract in the monkey most commonly have inhibitory fields located on the contralateral limb (Brown & Franz, 1969; Willis *et al.* 1974; Gerhart, Wilcox, Chung & Willis, 1981). However, intracellular recordings of SCT cells have revealed restricted inhibitory fields overlapping but eccentric to excitatory areas (Hongo *et al.* 1968; Brown *et al.* 1987). It has been suggested (Hongo *et al.* 1968) that this asymmetrical inhibitory field arrangement might provide a mechanism for detecting the direction of motion of a tactile stimulus on the skin.

In a previous study of PSDC neurones from the chloralose-anaesthetized cat a

small minority of units had receptive fields that expanded during the recording session, suggesting that the receptive field boundaries of PSDC neurones might be dynamically modulated (Brown *et al.* 1983). In the present experiments the receptive fields of PSDC axons were thoroughly examined for periods varying from 20 min to 1 h. During this time receptive field components were often reinvestigated on a number of occasions. Though edges of receptive fields, particularly those of light tactile excitatory components bordering on inhibitory fields, were often indistinct, unequivocal changes in receptive field boundaries were not detected. However, in the present experiments the skin of the hindlimbs was left intact and electrical stimulation of peripheral nerves, which apparently triggered some of the changes observed by Brown *et al.* (1983), was not employed.

Conclusions

The present results have shown that, at least in the chloralose-anaesthetized cat, a large proportion of PSDC neurones have complex receptive fields which differ in their organization from those of SCT cells (Hongo *et al.* 1968; Brown & Franz, 1969; Brown *et al.* 1987). These observations concur with reports of differences in the morphology and synaptic organization of PSDC and SCT neurones (Brown *et al.* 1977; Brown & Fyffe, 1981; Enevoldson, 1982; Maxwell *et al.* 1982, 1984, 1985; Bannatyne *et al.* 1987; but see Bennett, Nishikawa, Lu, Hoffert & Dubner, 1983). This combination of evidence suggests that the two somaesthetic systems employ different strategies of sensory processing in the dorsal horn, so that while several types of primary afferent fibre may influence neurones of both the PSDC and SCT systems in parallel, it seems likely that each may be organized to provide an optimal response to different aspects of cutaneous stimuli.

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