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RECEPTIVE FIELDS AND IN-FIELD AFFERENT INHIBITION OF NEURONES IN THE CAT'S LATERAL CERVICAL NUCLEUS

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SUMMARY

1. Extracellular microelectrode recordings were made from projection neurones of the lateral cervical nucleus (LCN) in cats anaesthetized with chloralose and paralysed with gallamine triethiodide.

2. The receptive fields of eighty-five units were analysed. Most units had excitatory receptive fields similar in size and shape to those of spinocervical tract (SCT) cells. A few (14%) had either very large fields or 'stocking-like' fields. The majority of the LCN neurones (fifty-five, 65%) were excited by hair movement and, in addition, by noxious mechanical stimulation within the skin area responding to hair movement. Twenty-five units (29%) were excited by hair movement alone. For seven of these twenty-five neurones, noxious mechanical stimulation within the excitatory receptive field produced inhibition of the background discharge. One unit was excited by noxious mechanical stimulation and for the remaining four units no receptive field could be found. In six units inhibitory receptive fields outside the excitatory field were found.

3. Air-jet stimuli were used to define the excitatory profiles of the units' receptive fields to hair movement. In general, receptive fields had single regions of greatest sensitivity usually at or near the centre of the field, where that was oval in shape, with the sensitivity declining towards the field's circumference. In some units with very large fields that included parts of one or two limbs and the trunk there could be more than one highly sensitive region.

4. Pairs of air-jet stimuli were used to investigate in-field afferent inhibition in LCN cells. One jet was used to condition the responses to another jet located at a different position within the excitatory receptive field and occurring 200 ms later. Sixteen units were tested and significant in-field inhibition was observed in all sixteen.

5. The in-field afferent inhibition was organized spatially in the sense that inhibition was generally strongest when the conditioning and testing stimuli were close together and became weaker as they were moved apart. The afferent inhibition was not simply a function of the response produced by the conditioning stimulus. Furthermore, increasing the strength of the stimuli did not in general lead to larger areas from which the inhibition could be produced. The inhibitory areas defined in these experiments were generally less than 120 mm in length in units with receptive fields much longer than 100 mm.

6. We conclude that: (1) neurones of the LCN that project through the medial lemniscus have the same classes of excitatory inputs as neurones of the SCT that excite them – there is no convergence from different classes of SCT cells onto LCN projection neurones; (2) the major, and perhaps the only, operation carried out at the level of the LCN is a considerable degree of spatial summation for a small subpopulation of neurones, although most LCN neurones have receptive fields no larger than those of SCT cells; (3) the in-field afferent inhibition described for SCT neurones is relayed through the LCN and there appears to be no spatial summation of the inhibition at this level since the inhibitory subfields are similar in size in both SCT and LCN cells.

INTRODUCTION

During the past 20 years the spinocervico-thalamic system in the cat has been well studied at the level of the spinocervical tract (SCT). Considerable information is now available on the location, density, distribution and anatomy of SCT neurones and on their physiological response properties (for reviews see Brown, 1981*a*, *b*). More recently our attention has been directed to a detailed analysis of receptive field properties of SCT cells and the synaptic coupling between hair follicle afferent fibres and SCT neurones (Brown & Noble, 1982; Brown, Noble & Rowe, 1986; Brown, Koerber & Noble, 1987*a*, *b*, *c*). Brown *et al.* (1987*b*, *c*) showed that transmission between a single hair follicle afferent fibre and a SCT cell was suppressed following activation, and this suppression could be evoked from throughout the excitatory receptive field of the SCT neurone and was not accompanied by signs of postsynaptic inhibition in the SCT cell. This phenomenon of in-field afferent inhibition has been analysed using air-jet stimuli (see the accompanying paper, Noble & Short, 1989) and it was shown that SCT excitatory receptive fields contain suppressive subdomains likely to correspond with the receptive fields of neurones intercalated between the hair follicle afferent fibres and the SCT cells. One of the objectives of the present series of experiments was to examine the target neurones of the SCT (the neurones of the lateral cervical nucleus (LCN)) for evidence of this in-field afferent inhibition and its organization after another series of synaptic relays.

The LCN, unlike the SCT, has received relatively little attention from neurophysiologists. Indeed, until very recently (Kajander & Giesler, 1987) neurones in the LCN were described as responding almost exclusively to hair movement and not to noxious stimuli. This was surprising since, in many different studies from a number of laboratories, SCT cells responding to both hair movement and noxious stimulation have been reported to make up between about 60 and 75% of any sample of SCT units with a further smaller group (up to 10% in some reports) responding only to noxious stimulation. In all reports on the responses of SCT cells only about 20–30% have been described as responding to hair movement alone. Kajander & Giesler (1987) have now shown that this lack of response by LCN neurones to noxious stimuli is almost certainly due to the use of barbiturate anaesthesia.

The present experiments (which were started before the report of Kajander & Giesler (1987) appeared) were designed to investigate the response properties of LCN neurones that projected through the medial lemniscus in order to determine what

operations the nucleus performs. Published work on the LCN in the cat (e.g. Oswaldo-Cruz & Kidd, 1964; Horrobin, 1966; Craig & Tapper, 1978; Metherate, da Costa, Herron & Dykes, 1986) had shown, mainly, that the only obvious difference between SCT and LCN neurones, apart from the above mentioned absence of responses to noxious stimuli, was an increase in the sizes of excitatory receptive fields. Furthermore, previous workers, except Fedina, Gordon & Lundberg (1968), had made little comment on the presence of inhibitory receptive fields for LCN neurones. Fedina *et al.* (1968), who used chloralose as the anaesthetic, had shown both postsynaptic and presynaptic inhibition at the level of the LCN. We were therefore interested to examine LCN cells for inhibitory fields, since these are a feature of SCT neurones (see Brown *et al.* 1987*c*).

A preliminary report of some of the results presented in this paper has been communicated to the Physiological Society (Brown, Maxwell & Short, 1988).

METHODS

Experiments were performed on nine adult cats (2·4–4·0 kg body weight) anaesthetized with α-chloralose (70 mg kg^{-1}) after induction of anaesthesia with halothane in a $N_2O:O_2$ mixture. Further doses of chloralose were given if required and the animals were paralysed with gallamine triethiodide during electrophysiological recording. Carotid arterial blood pressure was recorded from the left carotid artery (that on the side opposite to the lemniscal stimulation, see below) as was end-tidal CO_2 and rectal temperature. End-tidal CO_2 was kept within 3·5–4·0% by adjusting the rate and stroke volume of the respiratory pump and rectal temperature maintained with an electric blanket under the animal. Anaesthetic level was assessed by examining the degree of pupillary constriction and the continuous blood pressure record.

Laminectomies were performed from the first to the third cervical vertebrae inclusive and the most posterior parts of the occiput were nibbled away, thus exposing the dorsal column nuclei and the upper three cervical segments. The animal was fixed in a spinal frame, supported by two clamps, each gripping two adjacent vertebral spines in the thoracic and lumbar regions and the head placed in a stereotaxic head-holder. Traction was applied between the head and spinal frames and the head was ventrally flexed by 20 deg from the horizontal. A trephine hole was made in the skull on the right-hand side, centred on the A5 plane, and the dura retracted. The cortex was covered with a mixture of liquid paraffin and low-melting-point paraffin wax to prevent drying. Bilateral pneumothoraces were performed to improve cord stability.

Antidromic stimulation of the medial lemniscus. So that we could identify LCN neurones with axons projecting through the contralateral medial lemniscus, an array of stimulating electrodes was placed in the midbrain. The electrodes were sharpened tungsten wires, seven in number, insulated with epoxy varnish, mounted on a Perspex block and carried on a micromanipulator. The method used was that described by Gordon & Jukes (1964). The electrode array was constructed with the electrodes progressively longer from the lateral to the medial end of the row and was inserted at the Horsley–Clarke frontal plane A5 with the most medial electrode about 3 mm to the right of the mid-line. The electrodes were initially lowered to the horizontal plane H −4. Electrical stimuli (0·2 ms duration square waves) were applied between adjacent pairs of electrodes. In order to determine the most efficacious location for exciting the lemniscus, recordings were made with a silver ball electrode from the surface of the spinal cord over the left LCN (between C1 and C2) while the depth of the array was adjusted and different pairs of electrodes used for stimulating. The position of the array and the electrode pair to be utilized were fixed when the surface negative wave over the LCN was largest.

Electrophysiological recording from the LCN. Glass capillary microelectrodes filled with 4 M-NaCl (5–15 MΩ) were used to record extracellularly from LCN neurones. The electrodes were inserted usually between the C1 and C2 dorsal roots, on the left-hand side, and aimed at the LCN. Some recordings were made more rostral and more caudal to this, through the C1 or C2 dorsal rootlets. The contralateral medial lemniscus was stimulated as the recording microelectrode was advanced. Units were isolated that responded antidromically. Criteria for antidromic firing were: constant

latency of response, high frequency following of at least 500 Hz and, most importantly, collision between orthodromic and antidromic action potentials. Conduction distances from the stimulating electrodes to the recording site were measured at the end of each experiment.

Receptive field mapping and air-jet stimulation. The coat on the left-hand side of the animal was clipped. Receptive fields of LCN units were mapped with hand-held brushes, probes, tuning forks and with toothed clips. Excitatory fields were drawn on outline diagrams of the cat's body surface and examination was also made for inhibitory fields, which, if found, were also drawn on the figurines. The toothed clips provided stimulation that was mildly painful when applied to the experimenters' skin. Thermal stimulation was not used. Quantitative, timed, mechanical stimulation was provided with air-jet stimuli, usually of 4 mN force, as described in the accompanying paper (Noble & Short, 1989). In order to examine for in-field afferent inhibition, pairs of air-jet stimuli, with one location fixed and the other selected sequentially from the array of air nozzles, were used and the data analysed as described by Noble & Short (1989).

RESULTS

Receptive fields of LCN neurones

A total of eighty-six LCN units were recorded for which adequate receptive field examination was performed. A striking feature of the sizes of excitatory receptive fields of the LCN projection cells was that, in general, they were of similar size to those of the SCT. Indeed for fifty-eight of the eighty-six fields it would not have been possible, on the basis of field size alone (or on the excitatory inputs to the cells – see below) to have distinguished them from SCT cell receptive fields. We consider it important to stress this observation since it is easy to obtain the impression from the published literature that LCN cell fields are larger than those of SCT cells. We admit, however, that we have not performed a statistical analysis. Furthermore, we did observe receptive fields that were obviously different from those of the SCT. As reported by others, some LCN neurones have very large excitatory receptive fields that include most of a limb together with the major part of the trunk and even parts of both fore- and hindlimbs with intervening trunk. A second difference was the presence of LCN units with 'stocking-like' receptive fields on a limb. Again this is not observed for SCT units. In the present sample of LCN units, seven had very large fields of the former variety and five had 'stocking-like' fields. Examples of the smaller, SCT-like fields are shown in Fig. 1 and the large and 'stocking-like' fields in Fig. 2.

Another striking feature of the LCN receptive fields was that in terms of both excitatory and inhibitory input they fell into the same categories as SCT neurones. Thus, twenty-five units were excited by hair movement alone, fifty-five by both hair movement and noxious pinch, one by noxious pinch alone and for four units no receptive field could be found. The remaining unit had an excitatory receptive field that included most of the hindlimb and was excited by hair movement alone except for the part of the field on the most lateral toe from which excitation to pinch was also found (this sort of field has not been observed in the SCT). On a percentage basis, therefore, 29% were excited by hair movement, and 64% by hair movement and noxious pinch. If the units with no field and that responding to noxious pinch are grouped together (see the Discussion) then 6% fall into this category. These relative proportions are remarkably similar to those found in the SCT.

Inhibitory receptive fields were observed for a minority of units in the sample. The commonest inhibitory fields (seven units) were found for those neurones excited by

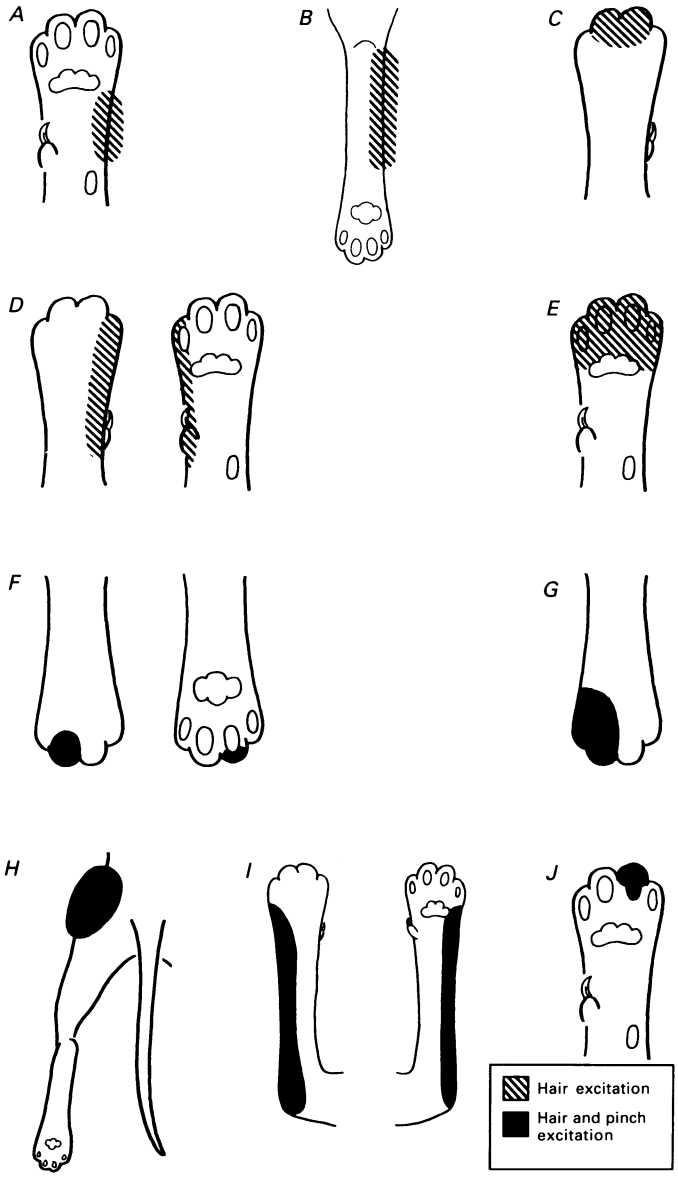

Fig. 1. Receptive fields of LCN cells. Examples of neurones with receptive fields consisting only of excitatory components and of a size similar to fields of spinocervical tract neurones. *A–E*, units excited by hair movement alone, *F–J*, units excited by hair movement and pinch.

hair movement alone. Inhibition was produced by noxious pinch within the area of the excitatory field responding to hair movement and appeared to be co-extensive with it (Fig. 3*A–C*). Three other units excited by hair movement alone had inhibitory fields that were located on skin separate from the excitatory field (Fig. 3*D* and *E*). Inhibitory fields were much rarer for units excited by hair movement and noxious pinch: only three of these, from the total of fifty-five units, had clearly defined

inhibitory fields and these were separated from or overlapped with the excitatory field (Fig. 3*F* and *G*). In a further two units excited by hair movement and noxious pinch, the initial application of a clip to the skin led to a short-lasting inhibition before an obvious excitation.

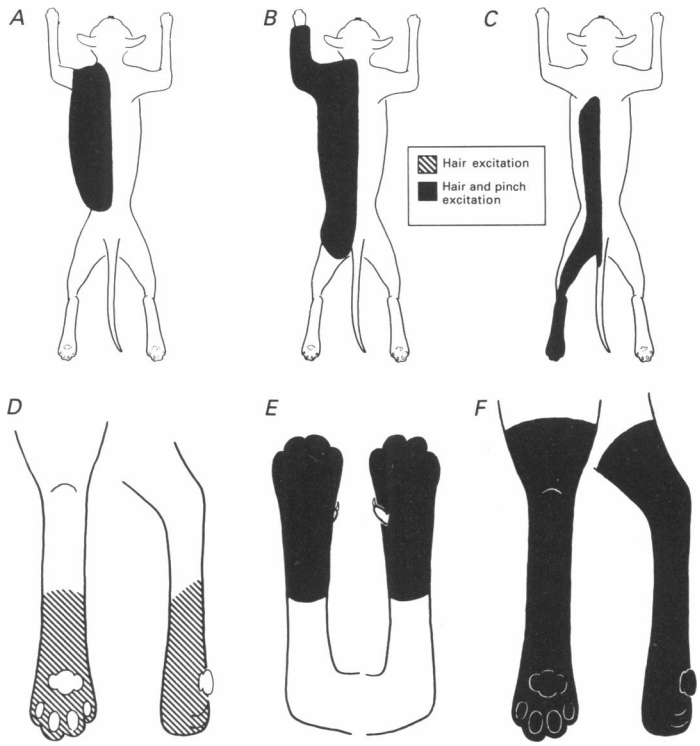

Fig. 2. Receptive fields of LCN cells. Examples of neurones with large receptive fields (*A–C*) and stocking-like receptive fields (*D–F*).

Conduction velocities of the axons of LCN neurones

The conduction velocities of the axons of LCN neurones ranged from 11 to 76 m s^{-1} with a modal value of 35–39 m s^{-1}. When the units excited by hair movement only and those excited by hair movement and noxious pinch were compared there was no statistical difference between the two subgroups (Student's *t* test) and both also had modal values of 35–39 m s^{-1}.

Excitatory response profiles of excitatory receptive fields of LCN cells

Response profiles were obtained to standard air-jet stimuli applied sequentially along a row of positions in the receptive fields of sixteen LCN cells. All units showed gradients of responsiveness across their receptive fields with the most sensitive part of the field usually at or near the geometrical centre (Fig. 4). For fields on part of a limb these profiles were generally unimodal but for fields encompassing the trunk and part of one or more limbs there were often several positions where the sensitivity was raised, leading to multimodal profiles (Fig. 5).

In-field afferent inhibition in LCN neurones

Sixteen units were extensively examined for in-field afferent inhibition using pairs of air-jets applied at different positions in the excitatory receptive fields with conditioning–testing intervals of 200 ms. In all sixteen units significant inhibition of the testing response was observed at some positions of the air-jets.

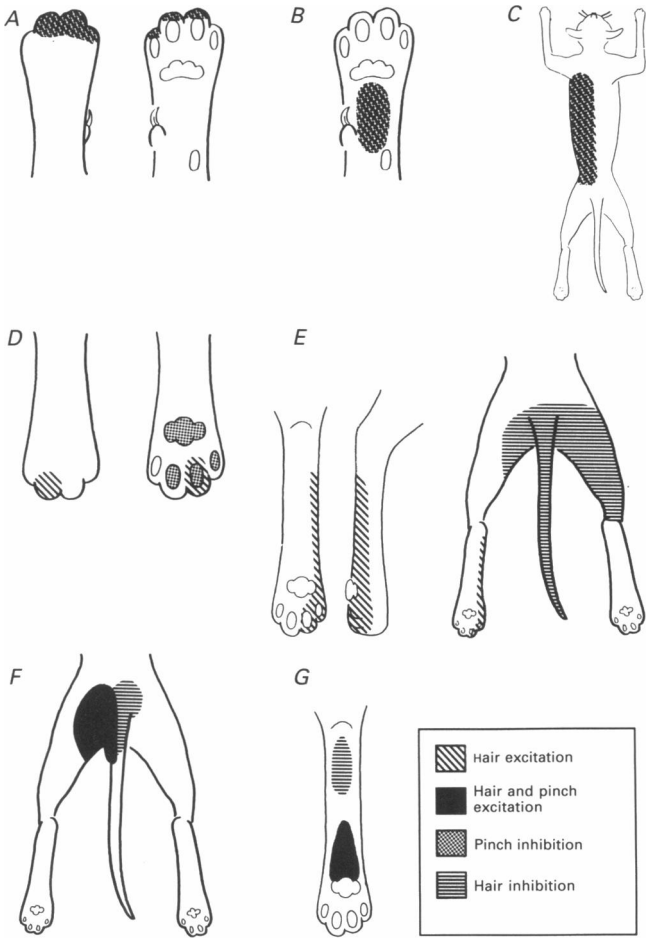

Fig. 3. Inhibitory components of receptive fields of LCN cells. *A–C*, units excited by hair movement and inhibited by pinch within the area excited by hair movement. *D* and *E*, units excited by hair movement and inhibited from outside the excitatory field. *F* and *G*, units excited by hair movement and pinch and inhibited from outside the excitatory field (by hair movement in these examples).

In-field afferent inhibition is organized spatially

When an array of conditioning air-jets was arranged across the long axis of an excitatory receptive field and used to condition responses from a fixed jet at or near the centre of the field, then the amount of inhibition produced was greatest when the conditioning jets were located close to the fixed central jet (Figs 6 and 9). For small

excitatory receptive fields limited to about 100 mm in their long axis this produced an inhibitory profile that usually more or less mirrored the excitatory profile.

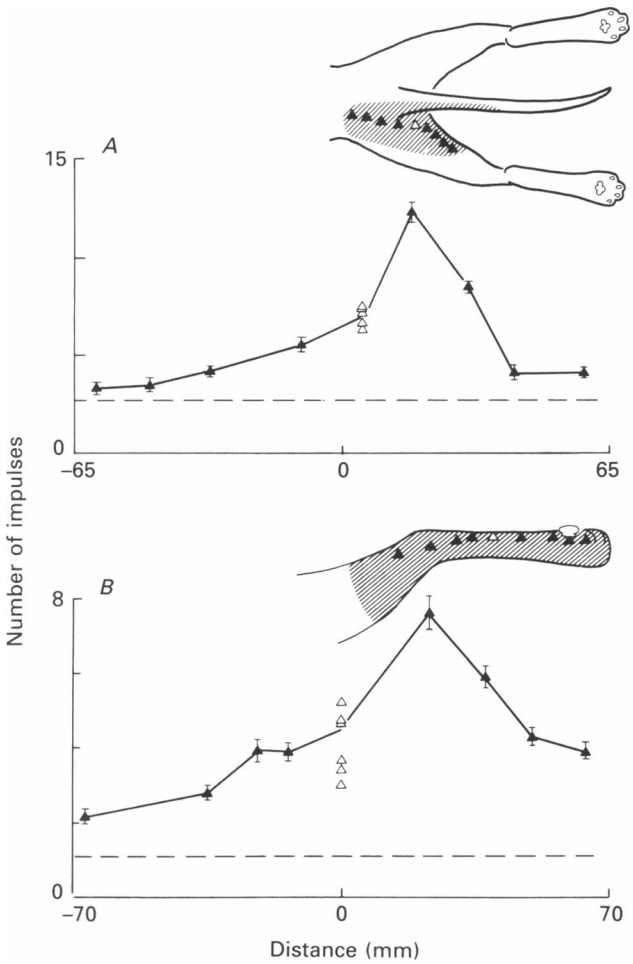

Fig. 4. Excitatory response profiles of the receptive fields of two LCN neurones to 4 mN air-jet stimuli. Examples of unimodal profiles. The figurines show the receptive fields and positions of stimulation. Each point on the graphs is the mean (with standard error bars) of fifty separate responses. The abscissa is the distance from the centre of the field (0); proximal, negative; distal, positive. The dashed line indicates the mean level of background activity per 100 ms.

Furthermore, in these circumstances, the inhibition produced by using the fixed central jet as conditioning stimulus for the other responses was similar to that produced when the response to the central jet was conditioned by the other air-jets (Fig. 6). This experimental protocol was the same as that used in the accompanying paper (Noble & Short, 1989) and the results give the impression that the degree of inhibition produced is dependent on the strength of the response evoked by the conditioning jet. Such a conclusion is incorrect as is shown when units with larger fields are examined and the locations of conditioning and testing stimuli are moved about.

For the unit illustrated in Fig. 7, the receptive field included most of the dorsal part of the trunk, the medial aspect of the posterior thigh and leg and the plantar surface of the foot and toes. The neurone was excited by hair movement and pinch within this large area. The excitatory response profile was unimodal with the most sensitive part at the level of the iliac crest. Seven different series of air-jet arrays were used to examine the effect of moving the conditioning–testing positions across the

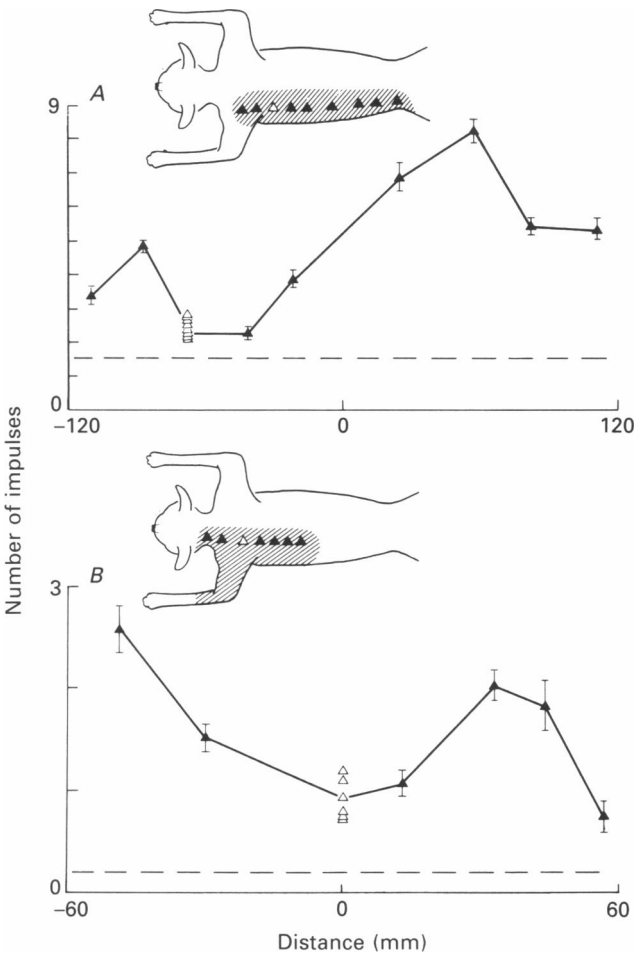

Fig. 5. Excitatory response profiles of the receptive fields of two LCN neurones to 4 mN air-jet stimuli. Examples of multimodal profiles. The figurines show the receptive fields and positions of stimulation. Each point on the graphs is the mean (±S.E.M.) of fifty responses. The dashed line indicates the mean level of background activity per 100 ms.

field. As can be seen from Fig. 7, all the inhibitory profiles demonstrated that inhibition was greatest when the conditioning and testing stimuli were close together and as they were moved away from the location of the most sensitive part of the field, then the inhibitory profiles moved appropriately. Even though the conditioning and testing stimulus locations were moved across the excitatory field so that each stimulus by itself evoked different responses (appropriate to the excitatory response

profile) the degree of inhibition produced when the conditioning and testing stimuli were close together was remarkably similar at points across the field, reaching amounts of inhibition of between 58 and 78% of control values except for one series at the most distal part of the receptive field. Furthermore, as the air-jet array was

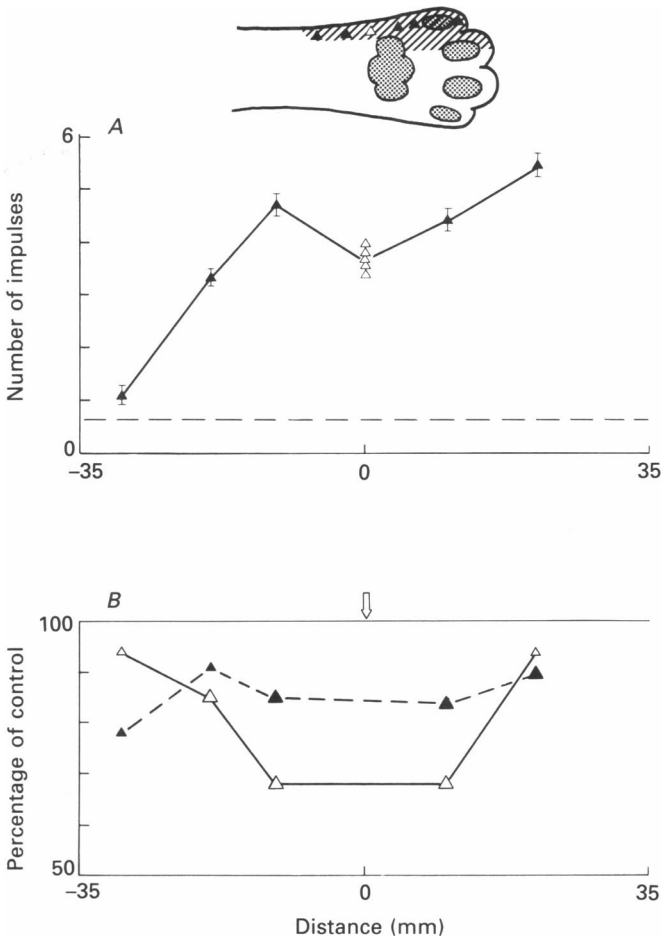

Fig. 6. In-field inhibition in an LCN unit with receptive field confined to less than 100 mm in length. The figurine shows the receptive field and the locations of the conditioning and testing sites. *A* shows the excitatory response profile for this unit, with the range of responses from the central position indicated. *B* shows the responses at the fixed point (arrow and open triangle on figurine) when conditioned from the testing sites (△) and the responses at the moving sites when conditioned from the fixed one (▲). The larger triangles indicate significant inhibition ($P < 0{\cdot}05$, Student's t test). In this unit the excitatory response profile was not unimodal – there was a 'hot spot' at the most distal site near the tip of toe 2. Each point is the mean of fifty responses.

moved to different positions, the inhibitory profiles generated from these different positions remained remarkably similar in extent, between 50 and 110 mm, except when positions on the hindlimb were tested when they increased to 130–140 mm. Finally, the inhibitory profiles were remarkably similar irrespective of whether the central (fixed) air jet was the conditioning or testing stimulus.

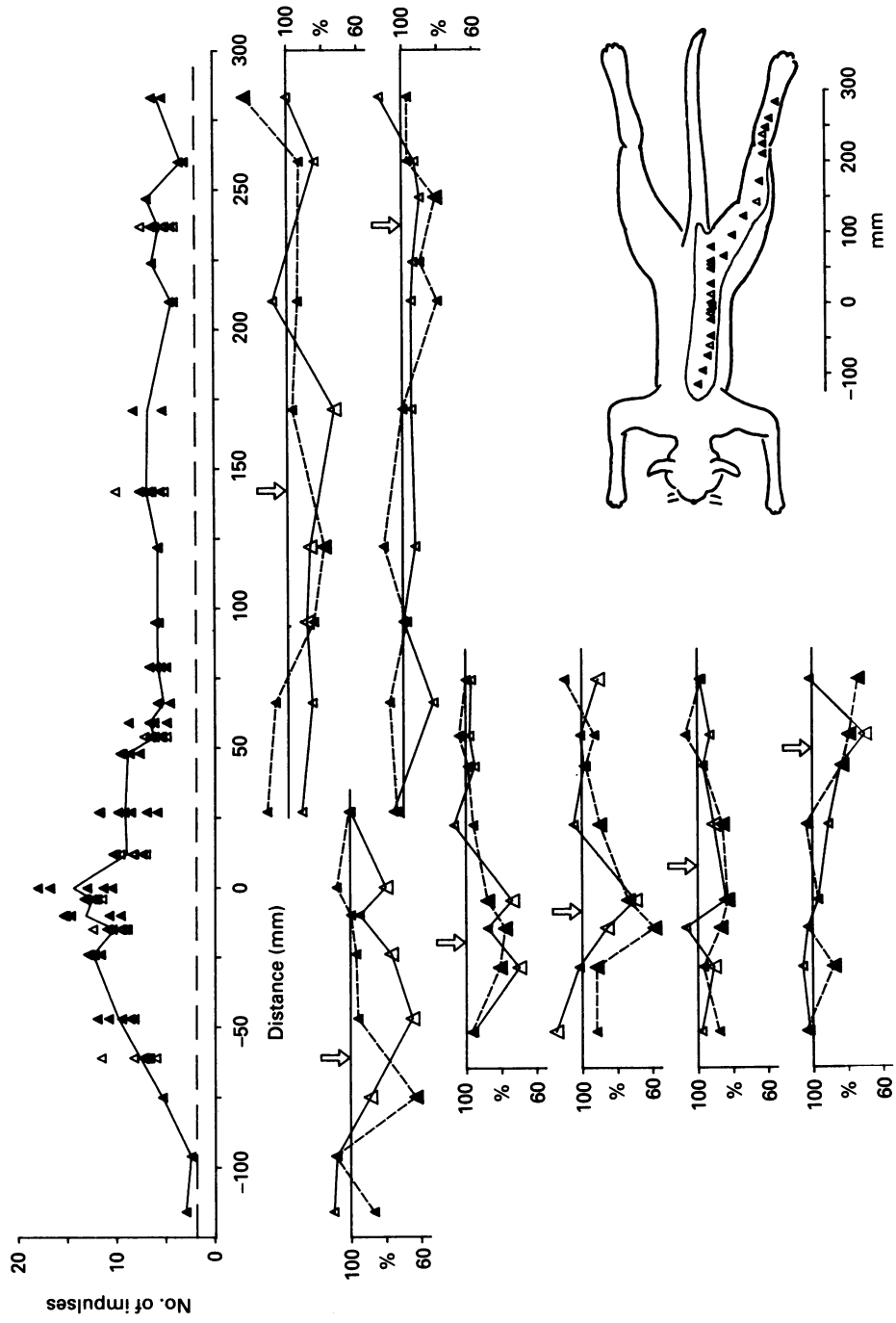

Fig. 7. In-field afferent inhibition in an LCN unit with very large receptive field. The upper panel shows the excitatory response profile, which was essentially unimodal. The lower panels show a series of inhibitory response profiles similar to Fig. 6*B*, in which the array of air-jets, and thus the conditioning and testing locations, was moved, in seven steps, across the total length of the field. The panels are arranged so that stimulation sites are in register with the upper panel. The seven pairs of inhibitory profiles (in each pair the fixed site was used as either conditioning and testing stimulus) show greatest inhibition where conditioning and testing sites are close together. Significant change ($P < 0{\cdot}05$, Student's t test) is indicated by larger symbols, and each point is the mean of fifty responses – the total number of responses recorded for this figure was 16 600. The figurine at the bottom right indicates the unit's receptive field and the stimulation sites.

Figure 8 summarizes all the data on the extent of inhibitory areas compared to the length of excitatory fields. Except for fields less than 100 mm long, all the points fall below the line of equality and very few inhibitory areas are greater than 120 mm long.

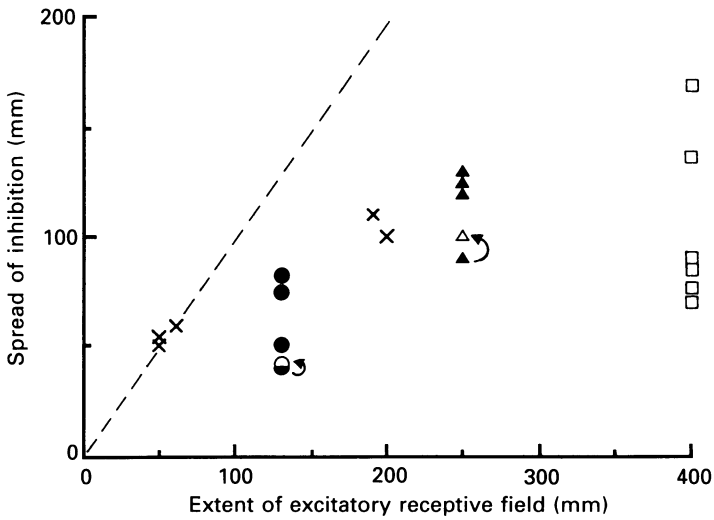

Fig. 8. Spatial spread of inhibition plotted against maximum extent of excitatory receptive field for eight units. The spatial spread of inhibition is limited to about 120 mm or less. The three sets of points plotted as circles, triangles and squares are each from one of three units that were extensively tested with different fixed points. In two of these latter units the conditioning and testing stimuli were increased (from the closed to the open symbol, indicated by arrows) and there was no marked increase in spread of inhibition. The dashed line, with a slope of unity, indicates where the points would fall if the inhibitory areas were co-extensive with the excitatory fields.

The spread of in-field afferent inhibition does not depend on stimulus strength

For all of the inhibitory profiles illustrated so far, the strengths of the conditioning and testing stimuli were not varied. It might be thought that increasing the strengths of the air-jet stimuli might lead to increased spatial effectiveness of the inhibition, especially if the degree of inhibition were directly linked to the strength of the afferent input. As shown in Figs 7 and 9, however, this is not so – at least for the strengths of stimulation used. When the strengths of conditioning and testing stimuli were increased to produce greater responses (Fig. 9) statistically significant inhibition remained essentially similar in extent even though the amount of inhibition was increased.

Time course of in-field afferent inhibition

In-field afferent inhibition in LCN neurones has a time course approaching 1 s in duration (Fig. 10). The unit illustrated in Fig. 10 also showed a phenomenon of some interest. Its excitatory field was on the medial foot and toe 2 (hindpaw) and the neurone was excited by moving hairs. It was also inhibited by both low-threshold

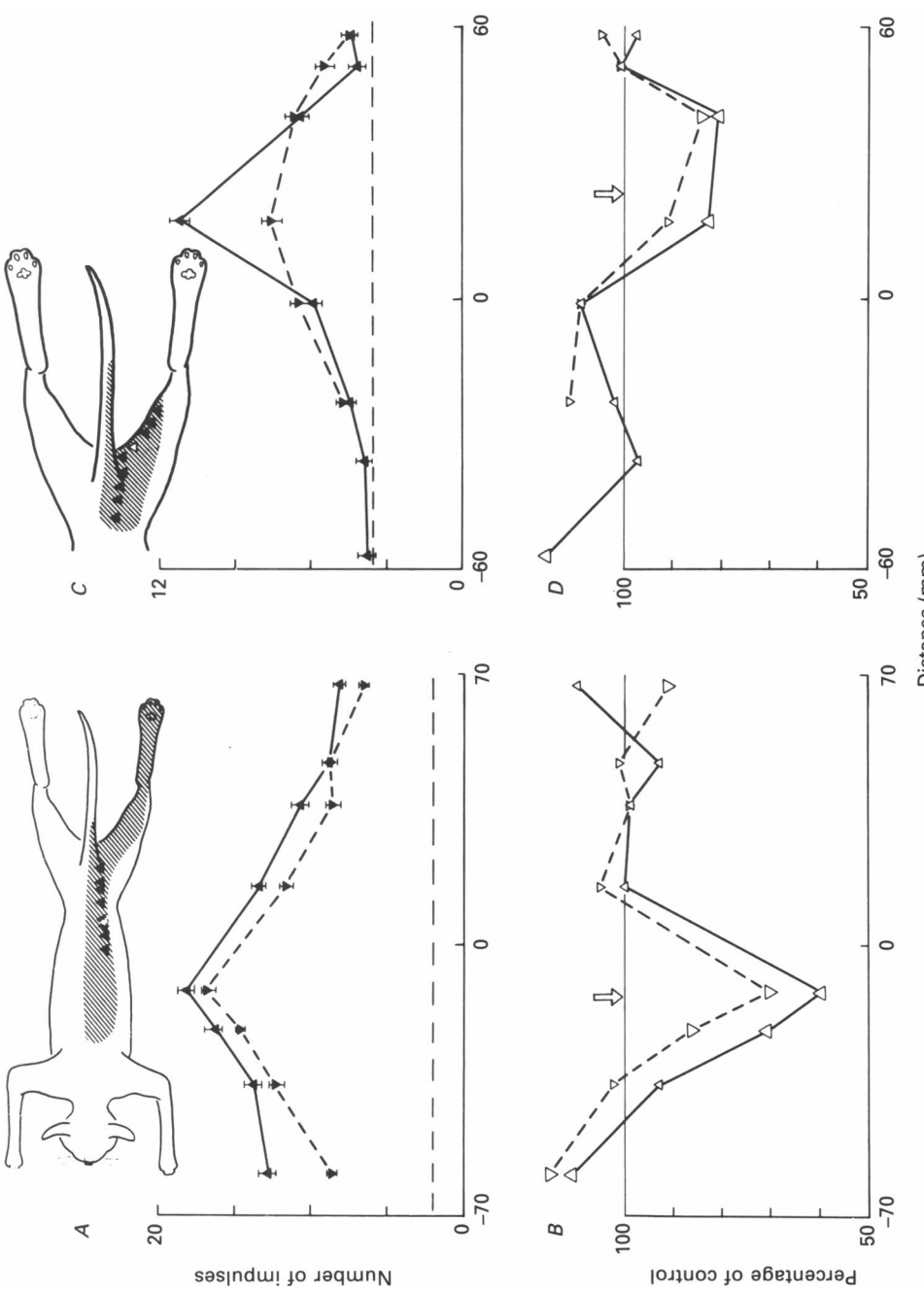

Fig. 9. In-field afferent inhibition in LCN units at different stimulus strengths. The figurines show the receptive fields and testing locations. The upper pair of graphs show the excitatory response profiles at two different strengths of air-jet stimulation (4 mN, ▲——▲; 8 mN, ▼– –▼). The lower graphs show the responses (4 mN, △——△; 8 mN, ▽– –▽) at the fixed point (arrows and open triangles on the figurines) when conditioned from the other points. Increasing the strength of the shocks, and therefore producing greater responses, increases the amount of inhibition but does not lead to marked expansion of the inhibitory subdomain (significant inhibition is shown by larger symbols). Each point is the average of fifty responses.

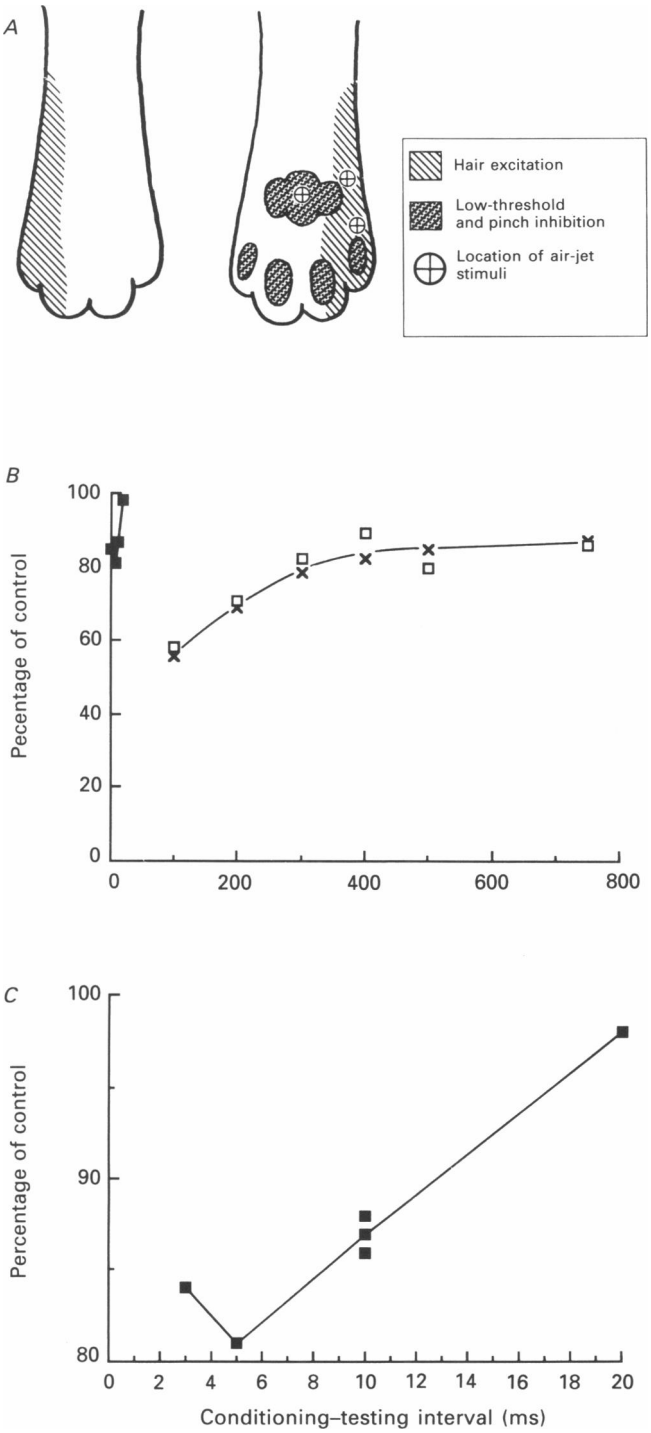

Fig. 10. For legend see opposite.

and high-threshold mechanical stimulation of all the toe pads and the central pad (Fig. 10*A*). We investigated the time course of inhibition evoked by low-threshold (air-jet) stimulation of the central pad. The results are shown in Fig. 10*B* and in more detail in Fig. 10*C*. The time course of the low-threshold inhibition from the glabrous skin of the central pad was very brief, inhibition being over by about 20 ms. Although we have only this single set of observations on this phenomenon, it is clear that this sort of inhibition is very different in character from the in-field afferent inhibition that is the main subject of the present paper. The short-lasting inhibition is likely to be due to postsynaptic inhibitory mechanisms.

DISCUSSION

The most striking observations of the present experiments were that the properties of projection neurones of the LCN are remarkably similar to those of the neurones from which they receive their input – those of the SCT. These similarities include receptive field size, receptive field excitatory and inhibitory components from the point of view of receptor types eliciting the excitation or inhibition and, also, the organization of in-field afferent inhibition. These similarities will be discussed in turn.

Receptive field size

Most reports of the properties of LCN neurones have stressed, to varying degrees, the presence of cells with large or very large receptive fields (Morin, Kitai, Portnoy & Dmirjian, 1963; Kitai, Ha & Morin, 1965; Horrobin, 1966; Craig & Tapper, 1978; Giesler, Urca, Cannon & Liebeskind, 1979; Metherate *et al.* 1986; Kajander & Giesler, 1987; see also the review by Boivie, 1983). Careful examination of most of these reports reveals that cells with very large fields made up only a small proportion of the total populations described. In our laboratory we have had considerable experience of SCT neuronal fields (including forelimb and trunk fields; Heath, 1978) and in our opinion only seven of eighty-six units (8%) had fields that were obviously larger than fields encountered for SCT cells. An additional five units (6%) had receptive fields that were different in terms of size or shape to those encountered in the SCT – these had 'stocking-like' fields that surrounded part of a limb.

Fig. 10. Time courses of in-field and out-of-field inhibition in an LCN neurone. *A* shows details of the receptive field organization of this unit. It was excited by hair movement on toe 2 and the medial hindfoot. It was inhibited by both low- and high-threshold mechanoreceptors of the glabrous toe pads and central pads. Air-jet stimuli were applied at the points indicated within the excitatory field and also on the central pad. *B* shows the time course of both the in-field and out-of-field inhibition. The in-field inhibition had a time course of about 700 ms and there was remarkable consistency irrespective of which air-jet stimulus was used for conditioning or testing. Conditioning–testing intervals of less than 100 ms could not be used as the test response began to merge with the conditioning response at values less than this. When the response to air-jet stimulation within the excitatory field was conditioned with an air-jet stimulus to the central pad a brief inhibition was observed (■) in *B*. This inhibition is shown in more detail in *C*, where it can be seen to have a peak at 4 ms and to last about 20 ms. Each point is the average response from fifty trials.

It would seem reasonable to conclude, therefore, that for the vast majority of LCN projection neurones (about 86% in the present sample) there is little evidence of excitatory convergence from SCT neurones leading to increased size of receptive fields at this level. Van Beusekom (1955) estimated that there are up to 3000 SCT axons entering each LCN, a number in agreement with calculations based on the relative proportions of SCT neurones with receptive fields on different parts of the body and the numbers in the lumbosacral cord (see discussion in Brown, Fyffe, Noble, Rose & Snow, 1980). The most recent estimate of the total numbers of mesencephalic projection neurones in the LCN gives values of about 8000 (Flink & Westman, 1986). There are, therefore, more projection neurones in the LCN than spinocervical afferent fibres entering the nucleus. Although these numbers, alone, cannot be used to predict convergence or divergence factors there is certainly no pressure towards convergence from the SCT to the LCN based on cell numbers.

A minority of LCN neurones projecting through the midbrain, however, does show evidence of convergence of input from the SCT that produces receptive fields larger in size and different in organization from those of SCT neurones. These are neurones either with very large receptive fields or with 'stocking-like' receptive fields. Both can be considered to handle input from skin surfaces not generally available to cells at the lower level, either from dermatomes widely separated (cervical and thoracic, thoracic and lumbosacral, cervical, thoracic and lumbosacral, etc. – the very large fields) or from dermatomes innervating the embryologically anterior and posterior parts of a limb (the 'stocking-like' fields). The receptive fields of these neurones, therefore, provide continuity of the body somatotopic map across large areas of that surface – a function that would seem to be necessary at some level in the somatosensory system.

Receptive field organization

The excitatory and inhibitory components of the receptive fields of projection neurones of the LCN are essentially the same as those of the SCT, their source of afferent input. Indeed, the similarities between the SCT and the LCN, both in the types of cutaneous receptors exciting and inhibiting them and in the arrangement of the excitatory and inhibitory components, are striking.

Thus at both levels most of the cells fall into two classes: those excited exclusively by hair movement (about 30% in both), and those excited by hair movement and, in addition, by noxious mechanical stimuli (about 65% in both). We did not examine responses to noxious heat but would expect the latter group to be excited by it. The remaining 5% or so of both SCT and LCN neurones in chloralose-anaesthetized cats either have no receptive field or are excited by noxious stimuli alone. It has been shown that this is a single group of neurones at the SCT level in which anaesthesia and/or the activity of descending neuronal systems leads to suppression of the responses to noxious inputs (Brown, 1971) and we suggest a similar explanation for these cells at the LCN level.

Excitatory receptive field profiles of LCN neurones were also similar to those of SCT cells, being usually unimodal with the most sensitive part of the field at or near the geometric centre of the sensitive area and the sensitivity falling off towards the

circumference of the field. Only in a small number of cells with large receptive fields were there sometimes additional sensitive peaks in the excitatory response profile.

Inhibitory receptive fields of LCN neurones were similar to those for SCT neurones. All types of inhibitory fields observed in the present series of experiments have also been recorded for the SCT, i.e. inhibition to noxious pinch evoked from the same area from which hair movement excites, inhibitory fields that are contained in hairy skin and overlap or are separated from the excitatory areas, and inhibitory areas on glabrous skin that are sensitive to either low-threshold mechanical stimulation, noxious stimulation or both (see Brown *et al.* 1987*c*). The organization of inhibitory fields of LCN cells is therefore similar to that of SCT neurones and, under the present set of experimental conditions, no additional inhibitory organization was discernible. In view of the presence of postsynaptic inhibitory potentials in LCN neurones and also the presence of presynaptic inhibition on the terminals of SCT axons (Fedina *et al.* 1968) additional inhibitory actions might have been expected. Further tests may be needed to reveal them.

In-field afferent inhibition in LCN neurones

When two air-jet stimuli were used, within the excitatory receptive field, one to condition the response from the other location, in-field afferent inhibition similar to that seen in SCT cells (Noble & Short, 1989) was observed. Its organization was similar to that in the SCT with a maximum spatial spread of about 120 mm even in LCN neurones with large or very large fields that included parts of the trunk and all of a limb or more. In the present experiments we examined this in-field afferent inhibition in more detail than previously and established that the spatial spread was not dependent on the responses to the conditioning or testing stimuli and also that throughout the excitatory field of an LCN neurone the in-field afferent inhibition was strongest when conditioning and testing stimuli were located close together.

Jänig, Schoultz & Spencer (1977), Jänig, Spencer & Younkin (1979) and Laskin & Spencer (1979) have carried out somewhat similar experiments to ours but recording from the dorsal column nuclei (cuneate), the thalamus and the somaesthetic cortex respectively. Their results establish the presence of in-field afferent inhibition at these sites but it appears to have a different spatial organization in comparison to that shown in this and the preceding paper (Noble & Short, 1989). Thus: (1) the inhibitory areas tended to extend beyond the excitatory ones; (2) inhibition was most effective when pitted against excitation from near the borders of the excitatory field (Jänig *et al.* 1977) even though the maximal inhibition was evoked from the receptive field centre (that is, the positions of maximal excitation and inhibition coincided); (3) no evidence for the presence of inhibitory subdomains within the excitatory fields were observed with the experimental protocol used.

The in-field afferent inhibition at the level of the LCN has a time course approaching 1 s in duration (another difference between this inhibition and that examined by Spencer and his colleagues, which has a much shorter time course). Operationally this means that an LCN neurone, especially one with a large excitatory receptive field, will respond less to a second restricted mechanical stimulus applied within about 50 mm and several hundred milliseconds than it did to an initial

stimulus, but should respond well to one applied outside these spatial and temporal limits. Furthermore, since the in-field afferent inhibition can be elicited from throughout the excitatory field and also produces relatively the same strength of inhibition from all pairs of closely located (10–20 mm) points in the field, its effect should be to sharpen up the excitatory profile to a stimulus moving across the field.

Conclusions

The major conclusion from the present set of experiments is that the properties of LCN neurones are largely set by the responses of the SCT neurones. The LCN maintains, for the most part, all the characteristics of operation of the SCT that determine receptive field size, excitatory response profiles, excitatory and inhibitory receptive field organization and the organization of the in-field afferent inhibition (that seems to reflect interneuronal operations on the SCT). The LCN must, for the time being at least, be considered as largely a true relay nucleus in this somatosensory pathway. At present the only additional operations performed at the level of the LCN are, for a small group of LCN neurones, the development of large receptive fields and 'stocking-like' receptive fields. If any other operations are performed at this level more sophisticated tests will be needed to reveal them.

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