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SOMATIC AND VISCERAL INPUTS TO THE THORACIC SPINAL CORD OF THE CAT: MARGINAL ZONE (LAMINA I) OF THE DORSAL HORN

BY F. CERVERO AND J. E. H. TATTERSALL*

From the Department of Physiology, Medical School, University of Bristol, University Walk, Bristol BS8 1TD

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SUMMARY

1. Single-unit electrical activity has been recorded from fifty-five neurones whose recording sites were located in or immediately adjacent to the marginal zone (lamina I) of the lower thoracic spinal cord (T8–T12) of anaesthetized or decerebrate cats. Their responses to stimulation of somatic and visceral afferent fibres and the sizes of their cutaneous receptive fields have been analysed and compared with the responses and receptive fields of neurones recorded throughout the spinal grey matter.

2. Neurones were classified according to their responses to innocuous stimulation of their somatic receptive fields (i.e. brushing and stroking) or to noxious stimulation (i.e. pinching, squeezing and/or heating above 45 °C). 52% of all the neurones recorded in lamina I were driven exclusively by noxious stimulation of the skin (nocireceptive); 33% were driven by both noxious and innocuous stimulation of the skin (multireceptive) and 15% were driven exclusively by innocuous stimulation of the skin (mechanoreceptive).

3. Visceral afferent inputs to these neurones were tested by supramaximal electrical stimulation of the ipsilateral splanchnic nerve (15 V, 0·2 ms, 0·3 Hz). Two types of neurone were distinguished according to their responses to visceral stimulation: (i) somatic neurones, driven only by stimulation of somatic afferent fibres and (ii) viscero-somatic neurones, driven by stimulation of somatic and visceral afferent fibres. Of the neurones recorded in lamina I, 33% were somatic and 67% were viscero-somatic. This proportion was very similar to the percentages of somatic and viscero-somatic neurones recorded throughout the grey matter (37 and 63%, respectively).

4. Viscero-somatic neurones in lamina I had somatic receptive field properties similar to those of viscero-somatic neurones of the entire spinal cord. Half of them were multireceptive, 39% were nocireceptive and 11% were mechanoreceptive. However, somatic neurones in lamina I had receptive field properties different from those of somatic neurones from other laminae: no multireceptive somatic neurones were recorded in lamina I; the vast majority (78%) were nocireceptive and 22% were mechanoreceptive.

5. The majority of somatic and viscero-somatic neurones in lamina I had small

* Present address: Chemical Defence Establishment (Biology Division), Porton Down, Salisbury.

somatic receptive fields but, even in this group of cells, viscero-somatic neurones had larger receptive fields than somatic cells.

6. Ascending axonal projections in both dorsolateral funiculi and in the contralateral ventrolateral quadrant were tested in eighteen lamina I neurones. Only one neurone was found to project to the cervical cord. This was a viscero-somatic neurone antidromically activated from the contralateral ventrolateral quadrant. The estimated conduction velocity of its axon was 15 m s^{-1}.

7. These results demonstrate substantial, but not absolute, viscero-somatic convergence on to lamina I neurones of the thoracic spinal cord. It is suggested that this may play a role in the spinal integration of visceral pain. In addition, a specific somatic nociceptive relay is preserved in lamina I even though this area receives many visceral afferent fibres.

INTRODUCTION

The most superficial layers of the spinal dorsal horn (the marginal zone or lamina I and the substantia gelatinosa or lamina II) have received considerable attention in recent years as the areas of relay and integration of the sensory input to the spinal cord mediated by fine afferent fibres (Cervero & Iggo, 1980; Dubner & Bennett, 1983; Willis, 1985). The particular relevance of these laminae in the processing of nociceptive information was highlighted by the discovery of neurones in the marginal zone specifically excited by somatic nociceptors (Christensen & Perl, 1970). Subsequent investigations have demonstrated the existence of a distinct group of lamina I neurones that relay their somatic nociceptive drives to the thalamus and other supraspinal regions and are subjected to central inhibitory influences (Cervero, Iggo & Ogawa, 1976; Cervero, Iggo & Molony, 1979*b*; Willis, 1985).

Many of these nocireceptive neurones of the superficial dorsal horn have also been found to have non-cutaneous inputs such as those activated by noxious stimulation of muscles and viscera (Cervero, 1983*a*; Craig & Kniffki, 1985). Anatomical studies have shown that fine afferent fibres from muscle and viscera project to the marginal zone but not to the substantia gelatinosa or to the dorsal horn laminae immediately ventral to it (Cervero & Connell, 1984; De Groat, 1986). This suggests that lamina I neurones could play a prominent role in the processing of somatic and visceral nociceptive information.

The activation of the nociceptor-specific neurones of the marginal zone by visceral inputs is of particular interest in the interpretation of the mechanisms of referred visceral pain, i.e. the referral to somatic structures of a painful sensation evoked by visceral stimulation. Such referral is commonly interpreted as being due to the convergence of visceral nociceptive inputs onto neurones driven by noxious somatic stimulation and projecting through somatosensory pathways (Ruch, 1946). Nocireceptive neurones in lamina I fulfil many of the requirements for a prime role in the spinal organization of referred visceral pain.

The present study was undertaken to examine the extent of viscero-somatic convergence in the marginal zone of the lower thoracic segments of the spinal cord. This region of the cord receives most of the visceral nociceptive afferent fibres from the upper abdomen as it is known that section or blockade of the visceral afferent

input to the thoracic cord results in visceral analgesia from the upper abdomen (see Cervero & Tattersall, 1986, for a recent review). In addition, we have studied the somatic receptive fields of lamina I neurones and the kinds of somatic stimulation that activate these cells, as very little information was previously available on the functional properties of superficial dorsal horn neurones of the thoracic spinal cord. Our approach was to compare the proportions of viscero-somatic neurones in the marginal zone and in the rest of the spinal cord and to study the functional properties of somatic receptive fields of superficial and deep neurones.

METHODS

Experiments were conducted on thirty adult cats of either sex with body weights between 1·6 and 4·2 kg. Twenty-four cats were anaesthetized with chloralose (60 mg kg^{-1} I.V.) after induction with either halothane (2·5% in one-third O_2 and two-thirds N_2O) or ketamine (20 mg kg^{-1} I.M.). Supplementary doses of chloralose were given to maintain an adequate level of anaesthesia. The other six cats were decerebrated by removing the forebrain rostral to the mid-collicular level under halothane anaesthesia (dose as before) which was discontinued after all surgical procedures to the animals had been completed. In all experiments, recordings of neuronal activity began not less than 6 h after the last administration of the short-acting induction anaesthetic. All animals were paralysed with gallamine and ventilated with a positive-pressure pump. The general methods for the monitoring and maintenance of the physiological state of the animals have been described previously in detail (Cervero, 1983*a*, *b*; Cervero & Tattersall, 1985). The lower thoracic spinal cord was exposed by a laminectomy from T6 or T7 to T13. In some animals, a second laminectomy was performed in the cervical region to expose the segments C1 to C4. The animals were mounted in a rigid frame and pools were made with skin flaps over the exposed areas of the spinal cord. Recording stability was improved by clamping the vertebral column, by infiltration of 2% agar around the spinal cord and by a bilateral pneumothorax. All spinal cord pools were covered with warm paraffin oil at 38 °C.

Recording techniques

Extracellular single-unit recordings were made through glass micro-electrodes filled with 4 M-NaCl (impedance measured at 1 kHz was 10–40 MΩ). Recordings were made from neurones in the right side of the grey matter of the segments T8 to T12. An ipsilateral dorsal rootlet was stimulated electrically (1–3 V, 0·1 ms, 1 Hz) through ball-tipped silver-wire electrodes when searching for neurones. Recordings were displayed on an oscilloscope and analysed 'on-line' and 'off-line' using a microcomputer (Cervero, 1985).

Stimulation of afferent fibres

Somatic afferent fibres were activated by natural stimulation of their receptive fields or by electrical stimulation through intradermal electrodes (10–20 V, 0·2 ms, 0·3 Hz). Natural stimulation included innocuous stimuli (i.e. brushing and stroking) as well as noxious (pinching, squeezing, heating above 45 °C and in a few cases application of ice). Visceral afferent fibres were activated by supramaximal electrical stimulation of the ipsilateral splanchnic nerve (15–20 V, 0·2 ms, 0·3 Hz). The right greater splanchnic nerve was dissected and prepared for electrical stimulation as described previously (Cervero, 1983*a*, *b*).

Stimulation of ascending pathways

Ascending somatosensory tracts were stimulated antidromically in fourteen experiments in order to identify neurones with axons in these pathways. Two sets of ball-tipped silver electrodes were placed on the ipsilateral dorsolateral funiculus at C1 and C3 and a concentric bipolar stainless-steel electrode (200 μm tip diameter, 500 μm tip separation) was placed in the contralateral ventrolateral quadrant at C2 level. In all these experiments the dorsal columns were cut at C4. Parameters of stimulation were adjusted to 100–200 μA, 0·2 ms and 1 Hz. Criteria for antidromic activation included the observation of collisions with orthodromically evoked spikes. Conduction distances were estimated as the minimum distance between stimulating and recording electrodes.

Histological methods

The position of the recording micro-electrode was marked by ionophoretic deposition of Pontamine Sky Blue in the last track of each experiment (Cervero, Iggo & Molony, 1979*a*). Several marks were made in this track at 1 mm intervals in order to provide a scale that would be subjected to the same amount of shrinkage as the rest of the tissue. The cord was then removed and fixed in 10% formaldehyde. The recording sites of the neurones were then calculated from these marks recovered in 80 μm transverse sections. This method has been extensively tested by marking some recording sites with Pontamine Sky Blue spots and estimating their location by reference to the scale marks. In one study, the error of locating recording sites with this method was shown to be not greater than 70 μm (Molony, 1978). The method has also been tested in this laboratory and the estimated locations were always found to be not more than 70 μm away from the marked spot. This error is comparable to the size of the lesion produced by passing current through a tungsten micro-electrode (e.g. see Craig & Kniffki (1985)).

The locations of stimulating sites in the cervical spinal cord were marked by passing 200 μA d.c. current through the ventrolateral quadrant electrode for 10–20 s. Locations were recovered in 100 μm transverse sections of the cord counter-stained with either cresyl violet or haematoxylin–eosin.

Comparative studies

One of the objectives of this investigation was to compare the properties of a sample of lamina I neurones with those of somatic and viscero-somatic neurones located in other spinal laminae. The latter neurones were taken from previously published data from this laboratory obtained in experiments with no particular recording bias, i.e. experiments in which somatic and viscero-somatic neurones were recorded from all spinal cord laminae including lamina I. The general properties of these sets of neurones have been described in detail in previous publications (Cervero, 1983*a*, *b*; Cervero & Tattersall, 1985; Tattersall, Cervero & Lumb, 1986). No differences in the receptive field properties described in this paper were observed between those neurones recorded in chloralose-anaesthetized cats and those recorded in decerebrate animals.

RESULTS

Sample of lamina I neurones

The results reported in this paper are based on a sample of fifty-five neurones recorded in or close to the marginal zone (lamina I) of the lower thoracic spinal cord (T8–T12). Thirty-three of these neurones were recorded in twenty-three experiments in which no particular emphasis was placed in recording from the superficial dorsal horn and, therefore, neurones were also recorded in other laminae. The remaining twenty-two lamina I neurones were recorded in seven cats in which sampling was restricted to the most superficial layers of the dorsal horn.

This sample includes all neurones whose recording sites, as assessed by our location method, were in or dorsal to the marginal zone. Excluded from the sample were all recordings of monophasic spikes with a very steep rising phase which were judged to originate from axons and not from cell bodies. Also excluded from the sample were those neurones whose responses to natural stimulation of their receptive fields were identical to the intracellularly identified 'inverse' neurones of the substantia gelatinosa (Cervero *et al.* 1979*a*) which have always been shown to be located in lamina II.

All neurones responded to electrical stimulation of the corresponding dorsal root and to electrical and/or natural stimulation of the skin of the corresponding dermatome (see Methods). Visceral inputs to all neurones were tested by supra-

maximal electrical stimulation of the ipsilateral splanchnic nerve (including greater and lesser branches). Fig. 1 shows some properties of one of the lamina I neurones in the sample including its responses to electrical stimulation of somatic and visceral afferent fibres, the location of its recording site and its somatic receptive field.

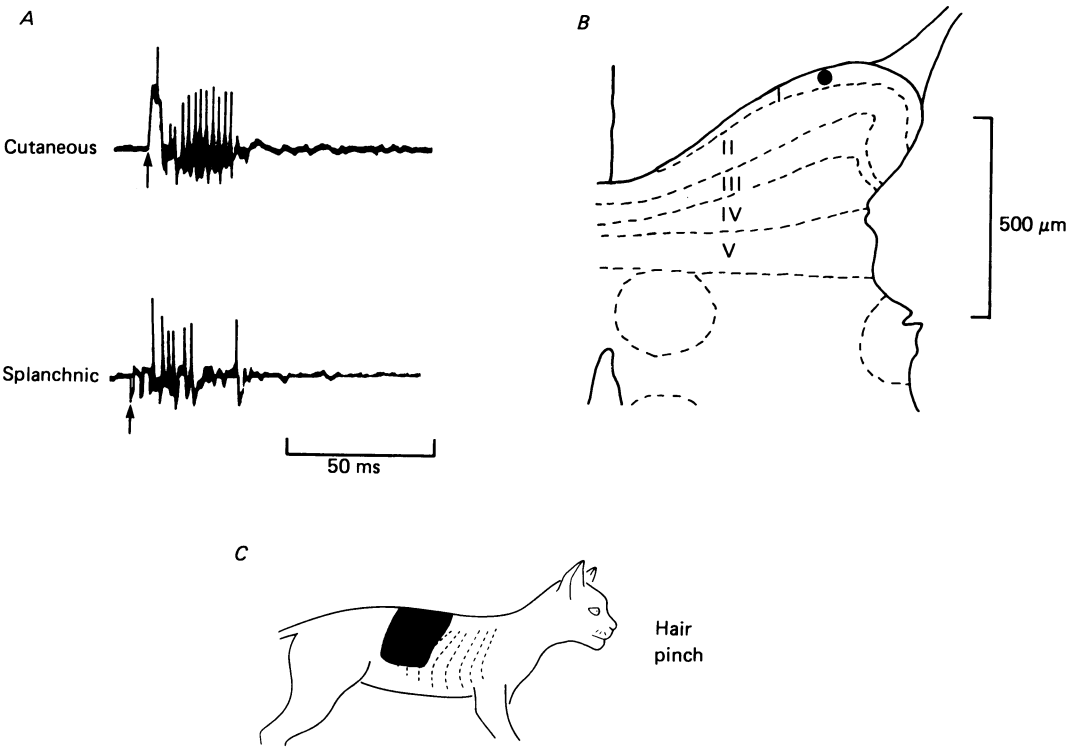

Fig. 1. A representative example of a viscero-somatic neurone recorded in lamina I of the lower thoracic cord. *A*, responses of this neurone to electrical stimulation of the skin (cutaneous) and of the splanchnic nerve (splanchnic). Stimuli were delivered at the times indicated by the arrows. *B*, location of the recording site of this neurone in lamina I. *C*, cutaneous receptive field of this neurone from which it could be excited by hair movement and by pinching the skin.

Viscero-somatic convergence

Two types of neurone were distinguished according to their responses to somatic and visceral stimulation: (i) somatic neurones, driven by somatic inputs but not by visceral stimulation and (ii) viscero-somatic neurones, driven by both somatic and visceral stimuli (Fig. 1).

Taking into account a sample of 303 neurones recorded from all spinal cord laminae, 37 % of them were somatic and 63 % were viscero-somatic (Fig. 2). In the present sample of lamina I neurones ($n = 55$) these proportions were: 33 % somatic and 67 % viscero-somatic (Fig. 2). Therefore, the proportion of viscero-somatic neurones in lamina I is similar to the average proportion of this type of neurone in all spinal cord laminae.

Locations of recording sites

The locations of the recording sites of eighteen somatic and thirty-seven viscero-somatic lamina I neurones are shown in Fig. 3. No differences were observed in the locations of these two sets of neurones. Most of the cells were recorded in the central

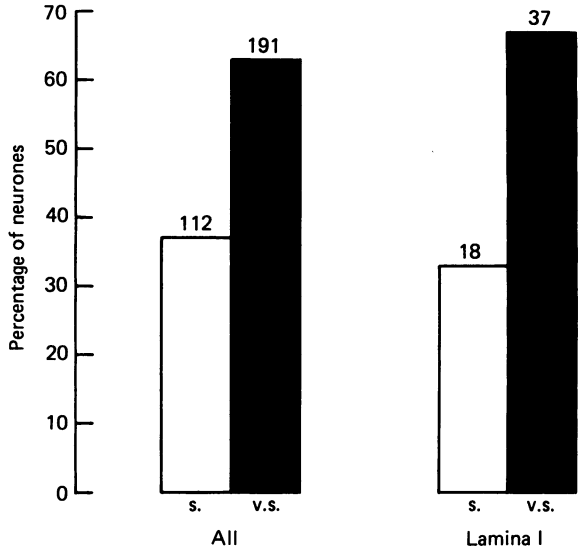

Fig. 2. Propertions of somatic (s.) and viscero-somatic (v.s.) neurones recorded in all spinal cord laminae (All) and in lamina I. Figures over the bars indicate number of neurones in each sample.

and lateral parts of lamina I which are the wider regions of the marginal zone. Very few neurones were recorded in the most lateral part of lamina I since recordings in this region were made difficult by the presence of afferent fibres running dorsoventrally from the dorsal root entry zone to Lissauer's tract. No recordings were made in the most medial part of lamina I which is very small area of tissue with no distinct ventral boundaries.

Somatic receptive fields

The somatic receptive fields of fifty-four lamina I neurones were examined and the kinds of natural stimulation of the skin that activated the neurones were noted (see Methods). The remaining neurone in the sample was lost before the full range of tests was completed. Receptive field properties of lamina I neurones were compared with those of a sample of 258 spinal cord neurones recorded in all laminae. In addition, lamina I and other spinal cord neurones were subdivided into somatic and viscero-somatic groups and the receptive field properties of these subgroups were also assessed. This data is presented in graphic form in Fig. 4.

Less than half of all spinal cord neurones (45%) were driven by noxious and innocuous forms of somatic stimulation (multireceptive). The remaining neurones

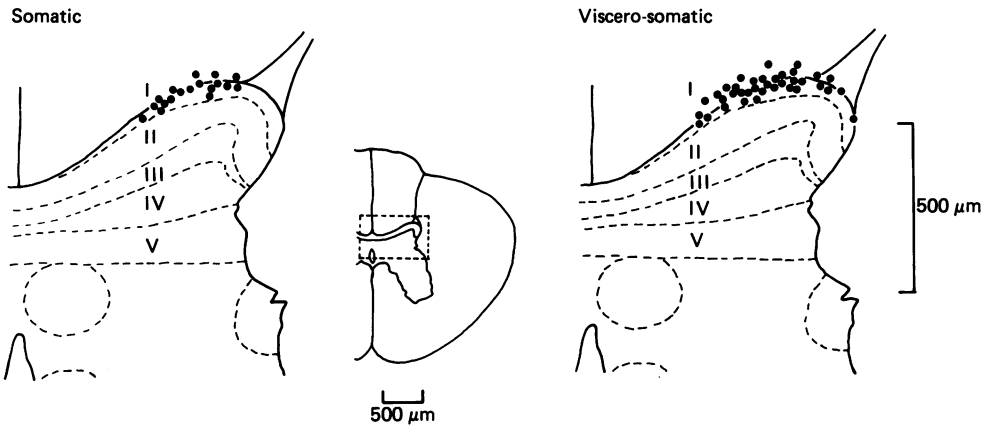

Fig. 3. Locations of the recording sites of eighteen somatic and thirty-seven viscero-somatic lamina I neurones. Locations have been pooled on standard transverse sections of the lower thoracic cord. The diagram at the centre of the Figure shows the outlines of the whole grey matter of this region of the cord.

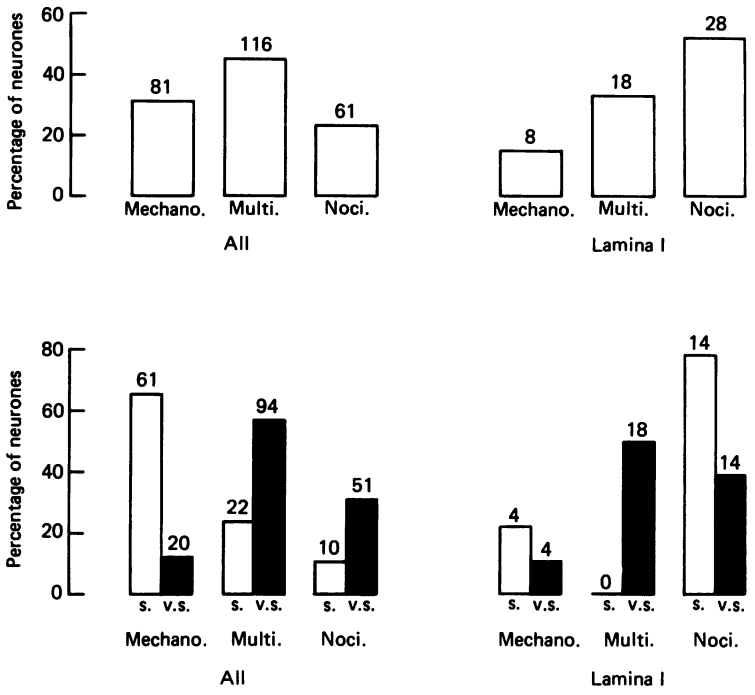

Fig. 4. Proportions of mechano-, multi- and nocireceptive neurones recorded in all spinal cord laminae (All) and in lamina I. The top histograms show the total sample of neurones and the bottom histograms display the same samples subdivided into somatic neurones (s.) and viscero-somatic neurones (v.s.). The figures over the bars indicate number of neurones in each sample. Note the absence of somatic multireceptive neurones in lamina I.

were divided into those responding exclusively to innocuous stimulation (mechanoreceptive, 31 %) and those responding only to noxious stimulation (nocireceptive, 24 %). In contrast, the majority of lamina I neurones were nocireceptive (52 %), with 33 % being multireceptive and only 15 % being mechanoreceptive.

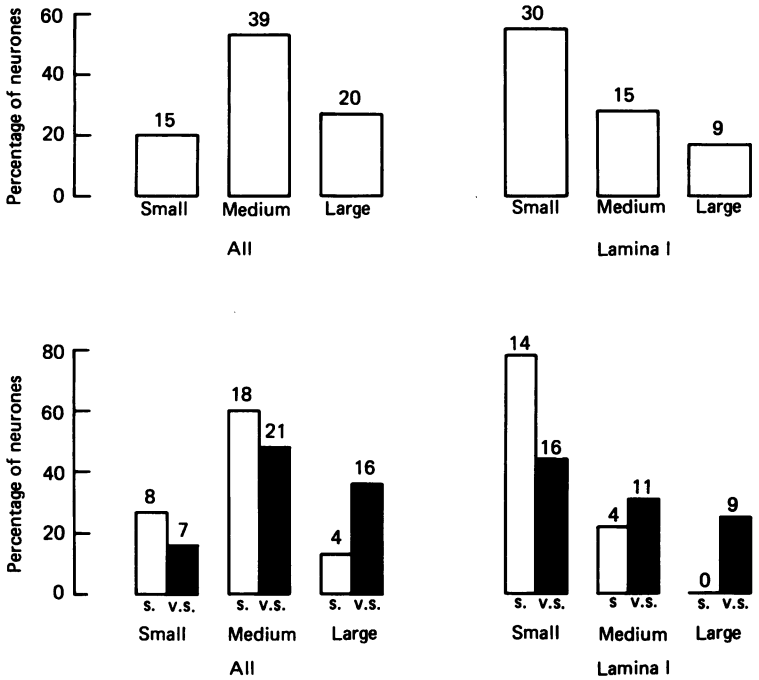

Fig. 5. Proportions of neurones with small, medium-sized and large receptive fields in all spinal cord laminae (All) and in lamina I. The top histograms show the total sample of neurones and the bottom histograms display the same samples subdivided into somatic neurones (s.) and viscero-somatic neurones (v.s.). The figures over the bars indicate number of neurones in each sample.

Greater differences in receptive field properties were observed when the presence or absence of a visceral input was taken into account. In the neuronal sample from the entire spinal cord, most viscero-somatic neurones had somatic nociceptive inputs (multireceptive = 57 % and nocireceptive = 31 %) and only a minority were mechanoreceptive (12 %). In contrast, most somatic neurones were mechanoreceptive (65 %), 24 % were multireceptive and 11 % were nocireceptive.

Viscero-somatic neurones of lamina I had receptive field properties similar to those of viscero-somatic neurones of the entire spinal cord. Half of them (50 %) were multireceptive, 39 % were nocireceptive and 11 % were mechanoreceptive. However, somatic neurones in this superficial lamina had receptive field properties markedly different from those of the sample taken in all spinal cord laminae. No multireceptive neurones with exclusive somatic inputs were recorded in the lamina I region and therefore all somatic neurones had specific cutaneous drives. The vast majority (78 %) were nocireceptive and the rest (22 %) were mechanoreceptive.

Size of somatic receptive fields

The boundaries of somatic receptive fields were measured and neurones were divided into three broad categories according to whether their receptive fields were small (less than 4 cm^2), medium sized (between 4 and 10 cm^2) or large (more than 10 cm^2). This data was obtained from fifty-four lamina I neurones and compared with the same properties of a sample of seventy-four neurones recorded in all spinal cord laminae. In addition, the neurones of both groups were subclassified according to the presence or absence of a visceral input to the cells. These data are presented in graphic form in Fig. 5.

Taking the sample of spinal cord neurones from all laminae, the majority of somatic and viscero-somatic neurones (53 %) had medium-sized receptive fields and most of the cells that had large fields were viscero-somatic. In contrast, the majority of somatic and viscero-somatic neurones in lamina I had small receptive fields (55 %). All lamina I neurones with large receptive fields (17 %) were viscero-somatic. Thus, lamina I neurones tend to have smaller receptive fields than other spinal cord neurones but, even in this group of cells, viscero-somatic neurones tend to have larger receptive fields than somatic neurones.

Axonal projections

Eighteen lamina I neurones (three somatic and fifteen viscero-somatic) were tested for ascending axonal projections by antidromic stimulation of tracts in both dorsolateral funiculi and in the contralateral ventrolateral quadrant at cervical levels. Only one of the tested neurones was antidromically driven from the cervical cord. This cell was a viscero-somatic neurone activated from the contralateral ventrolateral quadrant. The estimated conduction velocity of its axon was 15 m s^{-1}.

In a sample of eighty-eight spinal cord neurones from all laminae, ten (11 %) were found to have axonal projections in the dorsolateral funiculi or contralateral ventrolateral quadrant. This is a higher proportion than that found for lamina I neurones (one out of eighteen, 6 %) but this sample is not large enough to allow quantitative estimates of the proportion of projecting neurones from lamina I.

DISCUSSION

Four main observations have been made in the present study: (i) neurones in the marginal zone of the thoracic dorsal horn receive extensive viscero-somatic convergence, (ii) such convergence occurs more frequently onto neurones with a somatic nociceptive input, (iii) there is a small but distinct population of specific nociceptor-driven cells in lamina I without visceral inputs and (iv) receptive field sizes of all neurones in the marginal zone tend to be smaller than in other dorsal horn laminae.

An important point of interpretation of our data concerns the kind of neurone in the marginal zone from which recordings were made. We are certain that we recorded from post-synaptic elements for three reasons. First, the units responded with multiple spike discharges to single-shock electrical stimulation of afferent fibres. Secondly, all units had receptive fields considerably larger than the receptive fields

of single afferent fibres of the same modality (e.g. Fig. 1*C*). Thirdly, many cells responded to several modalities of stimulation including, in some cases, noxious and innocuous somatic stimuli as well as electrical stimulation of visceral afferent fibres. We are also confident that our recordings were taken in the vicinity of cell bodies and proximal dendrites because of the spike shapes (wide and biphasic spikes with inflexions in the rising phase), the short recording distances (usually less than 30–50 μm), the occasional intracellular penetrations showing post-synaptic potentials and the responses to somatic stimuli similar to those of intracellularly labelled lamina I neurones from other regions of the cord (e.g. Light, Trevino & Perl, 1979; Bennett, Abdelmoumene, Hayashi & Dubner, 1980; Molony, Steedman, Cervero & Iggo, 1981).

There is not enough anatomical data from the cat's thoracic cord to determine the likely cellular elements from which recordings were made. A recent morphological study (J. E. H. Tattersall & M. Rethely, in preparation) shows that the highest apparent cell density in this region of the cord occurs in the marginal zone. Several cell types coexist in this lamina including flat elongated cells similar to Waldeyer's Marginalle Zellen (Waldeyer, 1888; Lima & Coimbra, 1983, 1986) and smaller elements identical to those found in the outer substantia gelatinosa (Ramon y Cajal, 1909). It is also known that neurones at the origin of some ascending sensory pathways are located in this part of the thoracic dorsal horn (Willis, 1985) and we have some electrophysiological evidence for this. It is therefore most likely that our recordings were made from a heterogeneous population of neurones including marginal cells and other cell types present in lamina I. Because of the small size of the marginal zone and the fact that our recordings were largely extracellular, it is also conceivable that a few of the neurones included in the sample may have had their cell bodies in the outer substantia gelatinosa. However, our identification criteria excludes those neurones whose recording sites were found to be in the substantia gelatinosa, thus narrowing the sample to the most superficially located neurones.

Viscero-somatic convergence

There is some evidence that a very small minority of primary afferent neurones may have peripheral branches in somatic and in visceral nerves (Pierau, Fellmer & Taylor, 1984). However, there is no functional evidence for the presence of active sensory receptors at the end of these branches. Therefore, the extensive viscero-somatic convergence observed in the thoracic spinal cord must be mainly based on post-synaptic convergence of somatic and visceral primary afferents onto second-order neurones.

Transganglionic transport of horseradish peroxidase (HRP) through a variety of visceral nerves has demonstrated a consistent pattern of termination of visceral afferent fibres in the spinal cord (De Groat, 1986). The marginal zone (lamina I) and the ventral part of the nucleus proprius (lamina V) are the only dorsal horn areas that receive projections from visceral afferent fibres. A similar pattern of termination has been described for fine afferent fibres from muscle (Abrahams, Richmond & Keane, 1984; Nyberg & Blomqvist, 1984; Abrahams & Swett, 1986) and for small myelinated afferents connected to cutaneous mechano-nociceptors (Light & Perl,

1979). In addition, lamina I receives a dense projection from cutaneous Aδ and C afferent fibres (Cervero & Iggo, 1980).

These features of the afferent input to the marginal zone strongly suggest a prominent role of its neurones in the processing of somatic and visceral nociceptive inputs. Previous investigations have demonstrated convergence of cutaneous, muscle and visceral inputs onto lamina I neurones (Cervero, 1983*a*, *b*; Craig & Kniffki, 1985) including those at the origin of the spinothalamic tract (Craig & Kniffki, 1985; Willis, 1985). In our study we have confirmed the presence of substantial viscero-somatic convergence and have failed to find any cell driven exclusively by visceral afferent fibres. This supports the 'convergence–projection' theory of referred visceral pain (Ruch, 1946) which proposes that the referred sensation is due to visceral convergence onto somatosensory pathways in the spinal cord. Further support to this interpretation is given by our observation that most viscero-somatic neurones in lamina I have a somatic nociceptive drive either exclusively or, in some cases, in addition to a low-threshold mechanoreceptive input.

It is also interesting to note that viscero-somatic neurones in lamina I had generally larger cutaneous receptive fields than somatic neurones in the same region, even though as a whole lamina I neurones tended to have smaller fields than other dorsal horn neurones. This means that the somatic representation of those neurones presumably involved in the signalling of visceral pain is less precise than that of purely somatic neurones, which offers an explanation for the diffuse character of most visceral sensations.

Somatic neurones in lamina I

In spite of the relatively small size of the marginal zone and the presence in this area of visceral afferent projections, about a third of the neurones in our sample could not be driven by electrical stimulation of visceral afferent fibres. Moreover, this significant minority of lamina I neurones had receptive field properties different from those of viscero-somatic neurones of the same region.

It has already been mentioned that somatic neurones tended to have smaller receptive fields than viscero-somatic cells. Also, all the somatic neurones that we recorded in lamina I had specific cutaneous inputs either from low-threshold mechanoreceptors or, in the vast majority of cases, from cutaneous nociceptors. We did not test these neurones systematically for convergence from muscle afferent fibres and therefore we do not know whether these cells had somatic inputs other than from the skin. However, the bulk of the muscle input to the thoracic cord comes from the intercostal muscles which were available for mechanical stimulation in our experiments. We often encountered viscero-somatic lamina I neurones that responded to muscle squeezing or pinching. In contrast, the receptive fields of most somatic neurones appeared to be restricted to cutaneous structures. It would appear that the marginal zone of the thoracic dorsal horn contains a small group of neurones that receive a specific cutaneous input which, in most cases, comes from nociceptors.

Recordings from neurones in lamina I of other regions of the cord, particularly from lumbosacral segments, have sometimes shown multireceptive cells responding to several forms of cutaneous stimulation (the so-called 'wide dynamic range' neurones, see Willis, 1985). Very few of these studies have tested the responses of the neurones

to non-cutaneous inputs and therefore it is conceivable that multireceptive neurones in lamina I represent a form of convergence that may include non-cutaneous drives such as those from muscle or viscera. A recent study of muscle inputs to spinothalamic tract neurones in lamina I of the lumbosacral cord of the cat gives support to this interpretation (Craig & Kniffki, 1985).

In the trigeminal nucleus and in the lumbosacral cord some lamina I neurones are driven by sensitive thermoreceptors (Christensen & Perl, 1970; Dubner & Bennett, 1983; Craig & Kniffki, 1985). We did not test thoroughly for this type of input but we never observed responses in the non-noxious range when receptive fields were heated or cooled. The extent and magnitude of the thermosensitive input to the thoracic spinal cord remains to be studied in detail.

It can be concluded, from our observations and from the results of previous studies, that the marginal zone is an important area of relay and processing of the afferent input to the spinal cord mediated by fine afferent fibres from somatic and visceral organs. The visceral input to this lamina converges onto neurones that have somatic nociceptive inputs and relatively larger receptive fields. In addition, this region contains a group of somatic neurones whose inputs are restricted to a single modality of cutaneous receptor. In the majority of cases this input originates from cutaneous nociceptors.

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