TWO GROUP OF SPINAL INTERNEURONES THAT RESPOND TO STIMULATION OF THE ABDOMINAL VISCERA OF THE CAT

By S. B. McMAHON and J. F. B. MORRISON

From the Department of Physiology, University of Leeds, Leeds LS2 9JT

SUMMARY

1. Recordings have been made from sixty-three spinal interneurones that received inputs from the abdominal viscera. These were divided into two groups: group A were sacral interneurones without either significant ascending projections or afferent input from the lumbar splanchnic nerves and group B were neurones with short ascending axons and afferent inputs from the lumbar splanchnic nerves, and often also from the pelvic and pudendal nerves.

2. Somato-visceral convergence was common in both groups, and the somatic receptive fields of group A interneurones were in muscle and joints and less commonly skin innervated by sacral segments, whereas those of group B were innervated by lumbar and sacral segments.

3. Within both groups of neurones there was a proportion that showed no response to distension or contractions of the viscera, (despite the fact that they responded to visceral nerve stimulation), and those which did respond showed graded changes in discharge rate as intravesical pressure was raised. Some cells received inputs from only one viscus: the receptive fields of these cells are described as *simple* and the effect of raising the pressure in that viscus was either to excite or to inhibit the central neurone. Other cells received convergent inputs from two viscera: their receptive fields are described as *compound* and the effect of raising intraluminal pressures in the viscera allowed a further subdivision of these cells into two types. Type I cells were either excited or inhibited by distension or contractions of either viscus. Type II cells were excited by natural stimulation of one of the innervated viscera but inhibited by similar changes in the other. The static pressure thresholds of these cells were 9 ± 5 mmHg intravesical pressure, and 24 ± 11 mmHg intracolonic pressure (means $\pm$ s.d.).

4. It is proposed that within the population of neurones described there are cells (group A interneurones) that either mediate the vesico- and colono-sphincteric reflexes or the colono-vesical interactions that can be seen in the micturition reflex pathway.

5. It is proposed that the group B interneurones with short ascending projections mediate the vesico- and colono-sympathetic reflexes because their patterns of convergence, position in the spinal cord, latencies, and static pressure thresholds are consistent with those reflexes.

INTRODUCTION

There has been no systematic study of interneurones that might mediate spinal reflexes elictable from the bladder and colon. These reflexes mediate co-ordination of the internal and external sphincters of the urinary and gastrointestinal tracts, and modulate the sympathetic efferent influence on the tone of visceral and vascular smooth muscle, and possibly other structures. The aim of this study was to record from interneurones activated from the abdominal viscera in an attempt to elucidate the neural organiation of spinal visceral reflexes. Two groups of interneurones have been defined in the lumbo-sacral cord. Group A were located in sacral segments, did not have significant ascending projections, and did not receive inputs from the lumbar splanchnic nerves (i.e. from either the hypogastric or lumbar colonic nerve afferents). Group B had ascending projections that reached spinal segments that gave rise to the sympathetic outflow, and received inputs from lumbar splanchnic nerves. The function of these neurones is discussed.

METHODS

The experiments were performed on fifty-one cats, either decerebrated or anaesthetized with alpha-chloralose (60 mg kg^{-1}) or thiopentone (35 mg kg^{-1}) after initial induction with halothane. These animals also provided the data reported in McMahon & Morrison (1982a). Details of maintenance of anaesthesia, surgical procedures, and recording and stimulating techniques were essentially similar to those described in McMahon & Morrison (1982a). In the present experiments, however, recordings were made only from the sacral segments or from the white matter of the thoraco-lumbar segments T11–L1 of the cord. Units were isolated which responded to supramaximal stimulation of pelvic, hypogastric or lumbar colonic nerves, and which were not antidromically activated by stimulation of the spinal cord at C3. These units did not therefore have long projections. A diagrammatic summary of the innervation of the pelvic viscera is given in Floyd, McMahon & Morrison (1982).

Classification of units

In these experiments unitary recordings were obtained from two sites. The first was the white matter of thoraco-lumbar segments T11–L1. On the basis of their location and the criteria of Hunt & Kuno (1959), it appears likely that all of these recordings were made from axons of neurones. Since these units were not activated directly from C3, these recordings represent a class of interneurones with short ascending or descending projections. The second site was the grey and white matter of the sacral cord. On the criteria of Hunt & Kuno (1959) most of these recordings appeared to be of soma spikes. Although ventral root stimuli were not used to ascertain whether these neurones had an efferent axon, it is known that they were not autonomic efferents nor pudendal motoneurones because they were not driven antidromically from these sources. Also the position of the cells in the cord was not consistent generally with the location of somatic motoneurones.

The recordings therefore could represent interneurones either with a short ascending projection, as described above, or without such a projection and probably confined to the sacral cord. Some of the units had properties similar to those seen in recordings made from the thoraco-lumbar white matter, and these cells may well have had short ascending axons. However, most of the units had properties that were not seen in recordings made at thoraco-lumbar levels, and it is suggested that these are a separate group of interneurones which do not have significant projections.

RESULTS

Recordings have been made from sixty-three single neurones. The locations of forty-eight of these at the level of the recording electrode, determined as described

in the previous paper (McMahon & Morrison, 1982*a*), are shown in Fig. 1. In sacral cord recordings many units appeared to be in Rexed's laminae IV, V or VI, with most of the remainder widely distributed throughout laminae VII and X. At thoraco-lumbar levels, most units were situated in the lateral columns, concentrated in the intermediate positions.
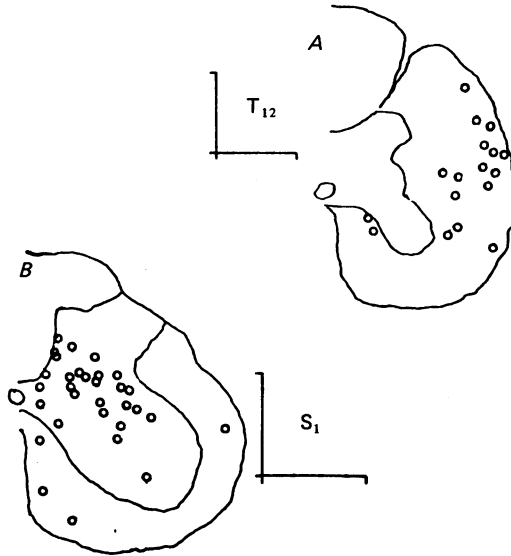

Fig. 1. Locations of forty-eight units within the spinal cord at the level of the recording electrode. *A* and *B* refer to recordings made from the thoracic and sacral levels of the cord respectively.

Resting activity

Most of the units studied (forty-eight out of sixty-three) exhibited background firing in the absence of apparent stimulation. The mean discharge rate of this firing was 12.2 ± 13.1 spikes/sec (mean $\pm$ S.D.). The interspike interval histograms of the resting activity showed exponential-like distributions at long intervals. The average resting discharge rates and proportion of units with no resting activity were found to vary between different types of preparation (decerebrate/anaesthetized) and between units which did and did not possess visceral mechanosensitive receptive fields. Thirty of the thirty-two units with visceral mechanosensitive receptive fields possessed some resting activity but only eighteen of thirty-one units without visceral mechanosensitive receptive fields showed resting activity. Units without visceral receptive fields were found predominantly in animals anaesthetized with alpha-chloralose, and it was these units that showed very low or no resting firing. These results were also in accordance with those observed for units with long projections (McMahon & Morrison, 1982*a*).

Responses to electrical stimulation of visceral nerves

The response of units to supramaximal electrical stimulation of pelvic, hypogastric or lumbar colonic nerves was tested. In order to uncover relatively weak inputs, short trains (four shocks with an interstimulus period of 5 msec) were sometimes employed.

Some units were also tested for their responses to pudendal nerve stimulation. The latencies, durations and magnitudes of evoked responses were calculated as in the preceding paper. Excitatory, inhibitory and most often, mixed responses were seen following visceral nerve stimulation. An example of a typical response and its associated post stimulus time histogram is shown in Fig. 2.
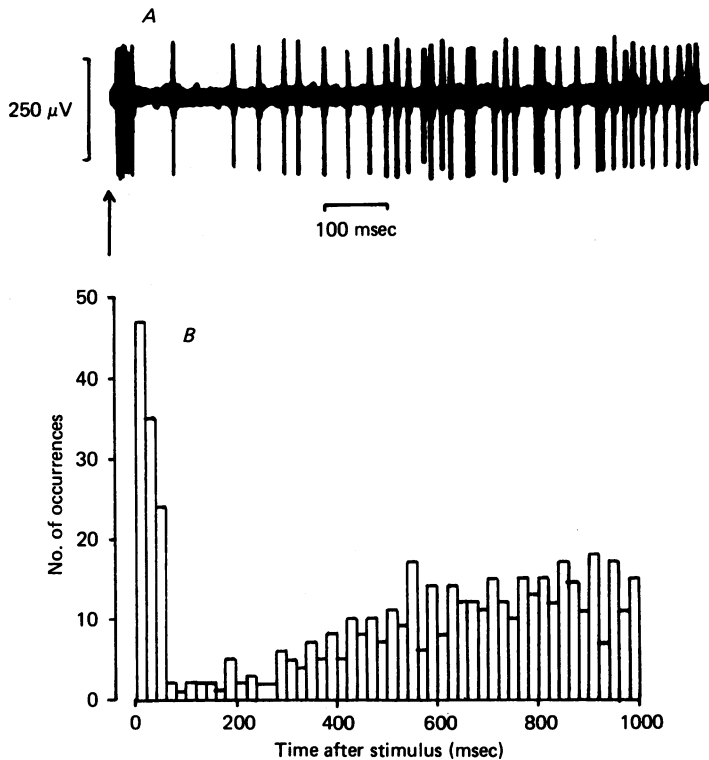

Fig. 2. *A*, the response of a unit to electrical stimulation of the pelvic nerves (10 mA, 1 msec pulse at the arrow). Five superimposed sweeps are shown. *B*, post-stimulus time histogram constructed from a series of sixty responses of the same neurone (20 msec bin width).

Convergence. Sixty of the sixty-three units were fully tested to establish their patterns of convergent input. Thirty-one of the sixty units showed inputs from more than one of the visceral nerves. However, this proportion was not reflected equally in recordings made at sacral and thoraco-lumbar levels as can be seen in Table 1.

The short ascending units recorded at thoracic levels were similar to the long ascending units described previously in that they mostly showed convergence from two or three of the visceral nerves stimulated (twenty-two out of twenty-nine units). In contrast, all of the thirty-one units recorded within the sacral cord received pelvic nerve inputs, but only nine showed convergence for hypogastric nerves or lumbar colonic nerves. This difference suggests that the population of units recorded at sacral levels is fundamentally different from those recorded at thoraco-lumbar levels, i.e. it is unlikely that many of the units recorded at sacral levels have short projections reaching thoraco-lumbar white matter.

Nature of responses to electrical stimuli. For units possessing background activity various patterns of response were seen, viz. excitation only, excitation followed by inhibition, excitation followed by inhibition followed by excitation, excitation followed by secondary excitation (after some interval). Units exhibiting primary inhibitory responses only rarely showed secondary excitatory responses. As with the units with long projections, where convergent inputs were present ($n = 31$) in nearly all cases ($n = 29$) the pattern of response from each effective nerve was the same.

TABLE 1. Patterns of convergence from peripheral visceral nerves. The proportion of units receiving inputs from one, two or three visceral nerves is shown. Units responding to only a single nerve have been divided according to which nerve was effective (PN, pelvic nerve, HGN, hypogastric nerve, LCN, lumbar colonic nerve)

	Single nerve			Convergence	
	PN	HGN	LCN	Two nerves	Three nerves
Short ascending units	2/29	4/29	1/29	12/29	10/29
Sacral units	22/31	0/31	0/31	7/31	2/31

TABLE 2. The latencies, magnitudes and durations of primary excitatory and inhibitory responses to visceral nerve stimulation, divided according to the level of the recording electrode and the nerve stimulated

	Short ascending units			Sacral units		
	PN	HGN	LCN	PN	HGN	LCN
Latency of excitatory response (msec)	19	13	13	14	33	19
Latency of inhibitory response (msec)	—	10	15	14	—	—
Magnitude of excitatory response (spikes/stimulus)	1·37	2·07	1·73	1·83	1·7	1·0
Magnitude of inhibitory response (% inhibition)	—	70	100	86	—	—
Duration of excitatory response (msec)	18	15	15	18	22	41
Duration of inhibitory response (msec)	—	70	50	500	—	—

Primary responses. Table 2 shows the average latencies, magnitudes and durations of both excitatory and inhibitory primary responses. In units recorded in the sacral cord the average latency of response to pelvic nerve stimulation was significantly shorter than the average latency to sympathetic nerve stimulation. The reverse was true of thoraco-lumbar recordings. Although there was no absolute distinction between classes, it can be seen that the average magnitude of excitatory responses and duration of inhibitory responses was greater for pelvic nerve responses in sacral recordings than for other responses, and the average magnitude of pelvic excitatory responses in the thoraco-lumbar recordings was slightly less than the magnitudes of response following sympathetic nerve stimulation.

Secondary responses. Secondary excitatory responses were rare. Secondary inhibitory

responses had, on average latencies of 52 msec and average magnitudes similar to those for primary responses. The duration of pelvic nerve inhibitory responses was greater in units recorded in the sacral cord than in units recorded in the thoraco-lumbar cord. Units recorded in the thoraco-lumbar cord showed slightly shorter durations of response during pelvic nerve stimulation than following hypogastric or lumbar colonic nerve stimulation. These differences, although qualitatively smaller, are similar to those seen for primary responses.
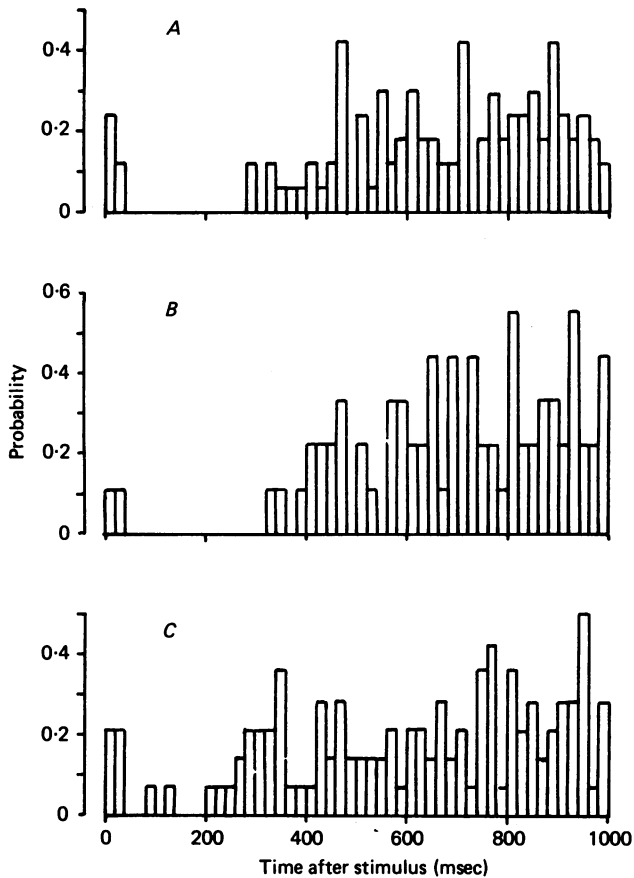

Fig. 3. Post-stimulus time histograms (20 msec bin width, 50 sweeps) obtained from one unit in response to electrical stimulation of the pudendal nerve (*A*), pelvic nerve (*B*) or hypogastric nerve (*C*). Probability was obtained by dividing the number of spikes in each bin by the number of stimuli given.

Responses to pudendal nerve stimulation

Twenty-two of twenty-four units tested responded to supramaximal stimulation of the pudendal nerve. The latency of response to pudendal nerve stimulation was, in nearly every case, similar to that seen following visceral nerve stimulation. Only one unit showed an input from the pudendal nerve but not from the pelvic nerve. Further, the latencies of evoked responses from the pelvic and pudendal nerves in

individual units were remarkably similar (correlation coefficient = 0·98, intercept non-significantly different from zero ($P > 0·10$)). Agreement between other visceral nerves and pudendal nerve latencies was not so good. The nature of the response following pudendal nerve stimulation was usually very similar to that seen following visceral nerve stimulation. An example of post-stimulus time histograms constructed from responses of one unit to stimulation of different visceral nerves is shown in Fig. 3.
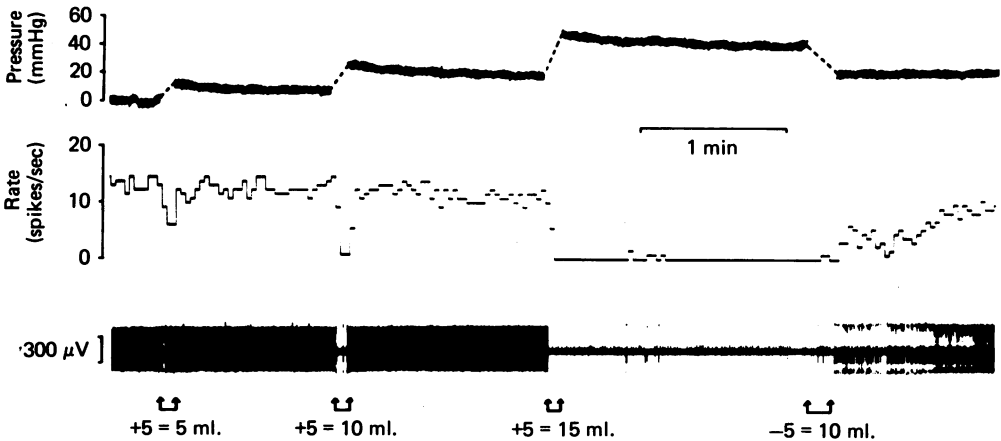

Fig. 4. Response of a unit to series of colonic distensions. The volumes injected and the total volume of the bowel segment are shown at the bottom. The spike train and derived spike rate are shown in the lower and middle traces respectively. The top trace shows intracolonic pressure.

Electrical thresholds

The electrical threshold (the lowest intensity of stimulation that produced a noticeable response) was determined for visceral nerves and found to be 1·65±0·16 mA (using single shocks) and 1·5±0·14 mA (using four shocks). The threshold for pudendal nerves was 1·0±0·1 mA when both one and four shocks were employed (all values mean±s.e.). From experiments where mass waves were recorded from visceral nerves or dorsal roots, it would seem likely that for all of the units examined in this study the largest diameter visceral afferents affecting the cells were of the Aδ class.

Responses to mechanical stimulation of the abdominal viscera

Of the sixty-three units, thirty-two were found to possess mechanosensitive visceral receptive fields. Responses could be slowly adapting or rapidly adapting and an example of a response is shown in Fig. 4. For units exhibiting slowly adapting responses, adapted discharge rates have been determined at various steady-state levels of intravesical or intracolonic pressure, as shown in Fig. 5. The differing form of the relationships, for different units suggests that populations as a whole may be able to signal accurately the level of visceral distension over a wide range of pressures. The minimum observed effective pressures at which units first showed changes in their

adapted discharge rates were 9 ± 5 mmHg for bladder distensions (mean $\pm$ s.d.) and 24 ± 11 mmHg for bowel distentions (mean $\pm$ s.d.).

Rapidly adapting responses showed an exponential-like decay in their discharge rates after the onset of stimulation. The half-time response for bowel stimulation was $3 \cdot 0 \pm 1 \cdot 4$ sec and for bladder distension $1 \cdot 8 \pm 0 \cdot 6$ sec (mean $\pm$ s.d.). Peak phasic responses in discharge rates tended to be much larger than adapted discharge rates. Active
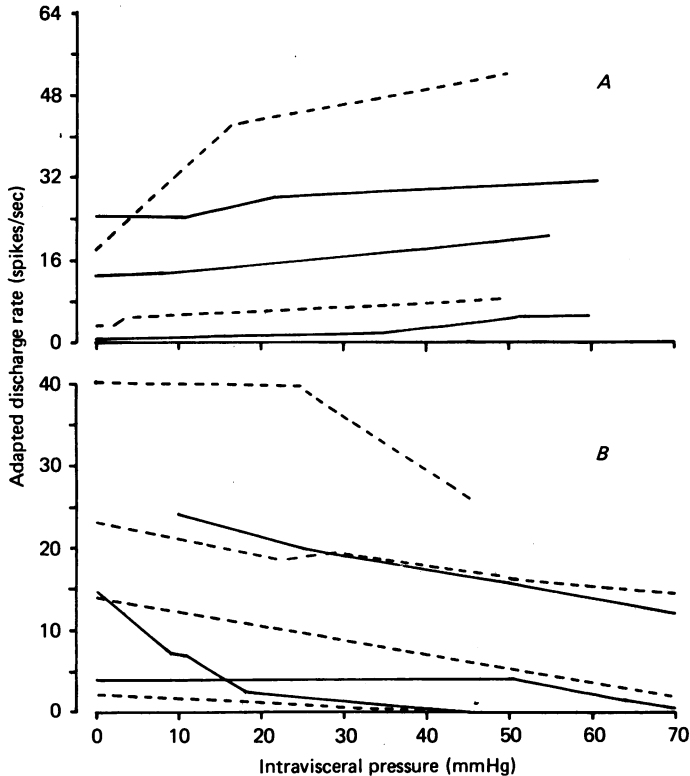
Fig. 5. Relationship between adapted discharge rates and intravisceral pressures for twelve units. The dashed and continuous lines derive from bladder and colonic distensions respectively. *A* shows responses of units that were excited by raising intravisceral pressure. *B* shows responses of units that were inhibited by raising intravisceral pressure.

contractions of the viscera produced responses which were qualitatively similar to those produced by passive distensions; however, the magnitude of such responses was invariably greater.

Receptive fields. The receptive fields of units could be confined to one viscus in which case they were designated *simple*, or could have components in more than one viscera, when they were designated *compound*.

In addition to this distinction, mechanical stimulation of the receptive fields could cause either an increase or a decrease in the firing rate of units, and the fields could then be considered excitatory or inhibitory.

In this study, twenty-one units had simple receptive fields, nine being excitatory and twelve being inhibitory. Eleven units had compound receptive fields, and these

were subdivided into type I ($n = 5$) where fields in different viscera were *both* excitatory or inhibitory, and type II ($n = 6$) where fields in different viscera were of different sign, i.e. one excitatory and one inhibitory.

No attempts were made to delineate the detail of receptive fields. However, some impression of the size and position of receptive fields was gained by probings and manipulations of the viscera. Receptive fields appeared very similar to those described for ascending units in the preceding paper (McMahon & Morrison,. 1982*a*); i.e. in the bowel they usually occupied the entire area of a segment of bowel up to 5 cm long, and were somewhat smaller in the bladder.

TABLE 3. Types of visceral receptive fields found in different classes of unit. $(+)$ and $(-)$ indicate excitatory and inhibitory fields respectively

	Short ascending units	Sacral units
Number of units with visceral mechanosensitive sites	14	18
No. of units with rec. field in one viscus only	11	10
No. of units with rec. fields in two viscera	3	8
No. with bladder $(+)$ fields only	2	2
No. with bowel $(+)$ fields only	2	3
No. with bladder $(-)$ fields only	6	4
No. with bowel $(-)$ fields only	1	1
No. with $(+)$ fields in both viscera	2	0
No. with $(-)$ fields in both viscera	0	3
No. with bladder $(-)$ and bowel $(+)$ fields	1	4
No. with bladder $(+)$ and bowel $(-)$ fields	0	1
Total no. $(+)$ fields	9	10
Total no. $(-)$ fields	8	16

Table 3 shows the distribution of receptive fields. In contrast to the long ascending units, a relatively large proportion of units recorded in the sacral cord possessed an excitatory field in one viscus and inhibitory field in the other.

Given the apparent differentiation between units in the sacral cord and those arising elsewhere, it seemed worthwhile to separate units according to the effective nerve input, as was done with the long ascending units. On this basis two groups have been found, viz. group A, receiving pelvic nerve input only; and group B, receiving input from sympathetic nerves. Nearly all of the cells in group B also responded to pelvic nerve stimulation. The majority of receptive fields in group A units were inhibitory, and a large proportion of excitatory fields occurred as components type II receptive fields. Group B units exhibited a more equal proportion of excitatory and inhibitory receptive fields. Most of the receptive fields in group B units without pelvic nerve inputs were excitatory.

Somato-visceral convergence

Fifty-four of the units were tested for responses to innocuous mechanical stimulation of cutaneous and deep structures. Nine units were also tested for their responses to nociceptive input by injections of small doses (10 or 15 μg) of bradykinin into the femoral artery. Table 4 shows the numbers of units responding to both noxious and innocuous somatic stimulation. Generally, most units with visceral receptive fields showed somato-visceral convergence.

TABLE 4. The numbers of units responding to innocuous somatic stimulation and injections of bradykinin (BK). The units are divided according to the level of the recording and the occurrence of visceral mechanosensitive receptive fields (VMRF)

	Sacral units		Short ascending units	
	VMRF	No VMRF	VMRF	No VMRF
No. responding to somatic stimulation	10	2	9	6
No. *not* responding to somatic stimulation	6	11	1	9
No. with receptive fields in hind limb/flank	2	0	7	6
No. with receptive fields in tail/perianal skin	10	2	2	0
No. giving *no* response to BK	0	4	0	2
No. giving increased discharge following BK	1	0	0	0
No. giving decreased discharge following BK	2	0	0	0
No. with somatic field and responding to BK	2	0	0	0
No. *not* responding to BK but with somatic receptive field	0	1	0	2

Somatic receptive fields were very similar to those described for long ascending units, i.e. many were 'deep', in muscle or joint. Fifteen units possessed receptive fields in the hind limb. In about two thirds of these units, receptive fields occurred unilaterally. The remainder of the units showed bilateral fields. The unilateral fields were most commonly restricted to one segment of limb, i.e. pressure on only one group of muscles or movement about only one joint was effective. For units possessing bilateral fields, fields in each limb were usually more extensive; movement about two or three joints usually being effective.

Fourteen units had receptive fields in the tail. Most fields appeared to be restricted to the proximal third of the tail, but in some cases extended over the complete length.

Units showing phasic responses to visceral stimulation often also showed phasic responses to somatic stimulation. There was no apparent correlation between the direction of visceral mechanosensitive receptive field present.

DISCUSSION

On the basis of their inputs and projections the cells in this study divide themselves into two groups: a population of sacral interneurones without significant ascending projections and without an input from the lumbar splanchnic nerves; and a group of lumbo-sacral neurones with short ascending axons which receive projections from the lumbar splanchnic nerves. The former population will be referred to as group A and the latter as group B neurones. The projection of the group B, or short ascending, units were to be found in the thoraco-lumbar white matter, and their properties were essentially the same as those of the long ascending units (McMahon & Morrison, 1982a) except that they did not project as far as the first cervical segment. The majority of cells in groups A and B gave responses to electrical stimulation of the pelvic and pudendal nerves, and the most common response was an excitatory burst followed by a period of inhibition of resting discharge, a pattern of events that was reported previously for other 'visceral neurones' by Fields, Partridge & Winter (1970). The latencies of the primary responses were uniformly consistent with the hypothesis that they were caused by activation of $A\delta$ axons in the peripheral nerves. Pelvic nerve stimulation caused more prolonged inhibitory effects in the sacral interneurones than in the short ascending neurones, and mechanical stimuli to the viscera caused inhibition in the former group more commonly than in the latter, whose receptive fields were more often excitatory. Somato-visceral convergence occurred more commonly from sacral segments in group A: in group B, a substantial proportion of somatic inputs were from lumbar segments.

Both populations can be subdivided according to the site and sign of the mechanosensitive receptive fields: receptive fields in one viscus only were *simple* or monovisceral, and could be excitatory or inhibitory; receptive fields with components in two visceral systems were *compound* or multi-visceral, and of two types: in type I, the receptive fields in different viscera were of the same sign, whilst in type II, they were of opposite signs. The receptive fields usually appeared large and diffuse which contrasts with the patterns of receptive field seen in primary afferents, which tend to have punctate and highly definable mechanosensitive sites (Morrison, 1973; Clifton, Coggershall, Vance & Willis, 1976; Floyd & Lawrenson, 1979). This suggests that several or many primary afferents impinge on to the units under study. The latencies of responses or cells with compound receptive fields were, on average, greater than those of cells with simple receptive fields; this may suggest that some of the latter may project on to the former cells.

Reflex pathways that may be mediated by group A interneurones

The reflexes that are initiated by visceral distension or contraction and are retained after a low lumbar spinal transection include the sphincteric reflexes and reflexes affecting the somatic musculature (Bishop, Garry, Roberts & Todd, 1956; Garry, Roberts & Todd, 1959; McPherson, 1966; Evans & McPherson, 1958). The latencies of pelvic-pudendal nerve reflexes are the shortest of all reflexes evoked from pelvic nerve afferents (Bradley & Teague, 1977; Floyd, McMahon & Morrison, 1979), and hypogastric afferents appear not to have any action on pudendal nerve efferents (unpublished observations). Some of the group A cells in this study had short latency

responses, and the lack of hypogastric projection is another feature that allows this group of cells to be associated with the sphincteric reflexes. The dominant effect of bladder or colonic distension on e.m.g. activity in the external sphincters and on the discharge of the group A interneurones was a marked inhibition. Some of these cells had compound type I receptive fields, which is consistent with the similarity of responses to distension of bladder and colon found in the external sphincters. The pressure thresholds for the activation of these units were within the range of pressures required to elicit the reflexes.

The presence of pudendal afferent inputs in group A cells is consistent with a role for these cells in sphincteric reflexes and in reflex inhibition of micturition contractions during stimulation of perianal or perineal skin (Kock & Pompeius, 1963; de Groat, 1975). Convergence of pelvic and pudendal afferents on the pudendal efferents that innervate the skeletal muscle spincters has previously been described by Bradley & Teague (1977). The latencies of response to pelvic and pudendal nerve stimulation were similar in that study and in the group A neurones described here.

The group A cells with compound type II receptive fields may be involved in the colono-vesical interactions described by de Groat (1971) and shown to depend on afferents in the colonic branches of the pelvic nerve by Floyd et al. (1982). McMahon & Morrison (1982b) proposed that one of the regulatory factors in micturition is a gating mechanism that is activated by vesical afferents and antagonized by colonic afferents in the pelvic nerve, and is unaffected by hypogastric nerve afferents. The patterns of convergence and the thresholds of group A interneurones are consistent with a role as mediators of this gating mechanism and as one determinant of micturition threshold.

Reflex pathways that may be mediated by group B neurones

Distension and/or contraction of the bladder or colon are known to produce either a rise or a fall in (1) arterial pressure (Mukherjee, 1957; Taylor, 1965), (2) the rates of firing of sympathetic efferents (de Groat & Lalley, 1972; Hick, 1979) and (3) the tone of the internal anal sphincter (Garrett, Howard & Jones, 1974) and of somatic muscles (Evans & McPherson, 1958). The group B neurones with simple receptive fields could be involved in any of these effects because of their short ascending projections that are required to carry information from the segments of afferent input to the upper lumbar and lower thoracic cord.

The vesico-sympathetic reflex described by de Groat & Lalley (1972) was elicited by pelvic nerve afferents, and the latency and site of the central pathway (in the lateral funiculus) as well as the intravesical pressure thresholds of the reflex (10–30 cm H_2O) were consistent with mediation by group B cells. S. B. McMahon, J. F. B. Morrison & K. Spillane (unpublished) found that a high proportion of sympathetic efferent units in the hypogastric nerve exhibited convergence from the pelvic, pudendal and the contralateral hypogastric nerve, and Hick (1979) has described that colonic and vesical afferents entering lumbar segments of the cord converge on, and have similar actions, on efferent units in the hypogastric nerve. Hick (1979) reported that the threshold pressures for the excitation of single sympathetic efferents were 8–32 mmHg intravesical pressure and 10–70 mmHg intracolonic pressure. These findings suggest that the pathway utilized by the vesico-sympathetic reflex of de

Groat & Lalley (1972) is a viscero-sympathetic pathway with convergence from afferents in the pelvic, pudendal and hypogastric nerves. Group B cells in this study fulfil the critera for such a role, and the presence of viscero-somatic convergence in these cells indicates that they could mediate the somato-sympathetic reflexes as well as the viscero-sympathetic reflexes that can be elicited from lumbo-sacral segments. A somato-sympathetic reflex involving afferents in the pudendal nerve has previously been described by Sundin, Carlsson & Knock (1974).

Only 2% of cells that received lumbar colonic nerve inputs in the present study did not exhibit convergence from other nerves: 6% also had inputs from the pelvic nerves, 28% from the hypogastric nerves, and 64% from both of these nerves. De Groat & Krier (1978) appear not to have studied the convergence of visceral afferents from different organs on to the lumbar colonic nerve efferents, but the possibility that there exists a substantial private pathway for lumbar colonic nerve afferents in the spinal cord seems remote. It is likely that the group B cells with type I compound receptive fields may be involved in convergent patterns of response from the colon and bladder, such as those found by Hick (1979). The thresholds of intracolonic pressure which activated group B neurones were comparable with those found in the pelvic nerve afferents from the colon (Floyd, Koley & Morrison, 1976; Floyd & Lawrenson, 1979) and in the colono-sympathetic reflex in the hypogastric nerve described by Hick (1979), but were less than those found to elicit a colono-sympathetic reflex by de Groat & Krier (1979).

Possible role in sensation. It is possible that many of these neurones could act as intermediaries in some of the long ascending pathways described by McMahon & Morrison (1982a); the latency of responses to electrical stimulation was shorter for these interneurones than for long ascending neurones. The mechanical thresholds of the units are within the range of pressures that elicit reflexes and non-painful sensations, and the stimulus response curve covers the range of pressures that induce pain.

REFERENCES

BISHOP, B., GARRY, R. C., ROBERTS, T. D. M. & TODD, J. K. (1956). Control of the external sphincter of the anus in the cat. *J. Physiol.* **134**, 229–240.

BRADLEY, W. E. & TEAGUE, C. T. (1972). Electrophysiology of pelvic and pudendal nerves in the cat. *Expl Neurol.* **35**, 378–393.

BRADLEY, W. E. & TEAGUE, C. T. (1977). Synaptic events in pudendal motorneurones of the cat. *Expl Neurol.* **56**, 237–240.

CLIFTON, G. L., COGGERSALL, R. E., VANCE, W. H. & WILLIS, W. D. (1976). Receptive fields of unmyelinated ventral root afferent fibres in the cat. *J. Physiol.* **256**, 573–600.

DE GROAT, W. C. (1971). Inhibition and excitation of sacral parasympathetic neurones by visceral and cutaneous stimuli in the cat. *Brain Res.* **33**, 499–503.

DE GROAT, W. C. (1975). Nervous control of the urinary bladder of the cat. *Brain Res.* **87**, 201–211.

DE GROAT, W. C. & KRIER, J. (1978). The sacral parasympathetic reflex pathway regulating colonic mobility and defaecation in the cat. *J. Physiol.* **276**, 481–500.

DE GROAT, W. C. & KRIER, J. (1979). The central control of the lumbar sympathetic pathway to the large intestine of the cat. *J. Physiol.* **289**, 449–468.

DE GROAT, W. C. & LALLEY, P. M. (1972). Reflex firing in the lumbar sympathetic outflow to activation of vesical afferent fibres. *J. Physiol.* **226**, 289–309.

EVANS, M. H. & MCPHERSON, A. (1958). The effects of stimulation of visceral afferent nerve fibres on somatic reflexes. *J. Physiol.* **140**, 201–212.

FIELDS, H. L., PARTRIDGE, L. D. & WINTER, D. L. (1970). Somatic and visceral receptive field properties of fibres in ventral quadrant white matter of cat spinal cord. *J. Neurophysiol.* **33**, 827–837.

FLOYD, K., KOLEY, J. & MORRISON, J. F. B. (1976). Afferent discharges in the sacral ventral roots of cats. *J. Physiol.* **259**, 37P.

FLOYD, K. & LAWRENSON, G. (1979). Mechanosensitive afferents in the cat pelvic nerve. *J. Physiol.* **290**, 51P.

FLOYD, K., MCMAHON, S. B. & MORRISON, J. F. B. (1979). Inhibitory interactions between the colonic and vesical branches of the pelvic nerve in the cat. *J. Physiol.* **290**, 50–51P.

FLOYD, K., MCMAHON, S. B. & MORRISON, J. F. B. (1982). Inhibitory interactions between colonic and vesical afferents in the micturation reflex of the cat. *J. Physiol.* **322**, 45–52.

GARRETT, J. R., HOWARD, E. R. & JONES, W. (1974). The internal anal sphincter in the cat: a study of nervous mechanisms affecting tone and reflex activity. *J. Physiol.* **243**, 153–166.

GARRY, R. C., ROBERTS, T. D. M. & TODD, J. K. (1959). Reflexes involving the external urethral sphincter in the cat. *J. Physiol.* **149**, 653–665.

HICK, V. E. (1979). Vesico-sympathetic reflexes mediated by hypogastric nerve afferents in the cat. *J. Physiol.* **290**, 49P.

HUNT, C. C. & KUNO, M. (1959). Properties of spinal interneurones. *J. Physiol.* **147**, 346–363.

KOCK, N. G. & POMPEIUS, R. (1963). Inhibition of vesical motor activity induced by anal stimulation. *Acta chir. scand.* **126**, 244–250.

LANGLEY, J. N. & ANDERSON, H. K. (1895). The innervation of the pelvic and adjoining viscera. Part I. The lower portion of the intestine. *J. Physiol.* **18**, 67–105.

LANGLEY, J. N. & ANDERSON, H. K. (1896). The innervation of the pelvic and adjoining viscera. Part II. The bladder. *J. Physiol.* **19**, 71–84.

MCMAHON, S. B. & MORRISON, J. F. B. (1982a). Spinal neurones with long projections activated from the abdominal viscera of the cat. *J. Physiol.* **322**, 1–20.

MCMAHON, S. B. & MORRISON, J. F. B. (1982b). Factors that determine the excitability of parasympathetic reflexes to the cat bladder. *J. Physiol.* **322**, 35–43.

MCPHERSON, A. (1966). The effect of somatic stimuli on the bladder in the cat. *J. Physiol.* **185**, 185–196.

MORRISON, J. F .B. (1973). Splanchnic slowly adapting mechanoreceptors with punctate receptive fields in the mesentery and gastrointestinal tract of the cat. *J. Physiol.* **253**, 349–361.

MUKHERJEE, S. R. (1957). Effect of bladder distension on arterial blood pressure and renal circulation in acute spinal cats. *J. Physiol.* **138**, 300–306.

SUNDIN, T., CARLSSON, C. & KOCK, N. (1974). Detrusor inhibition induced from stimulation of the anal region and from electrical stimulation of pudendal nerve afferents. *Investve Urol.* **5**, 374–378.

TAYLOR, D. F. M. (1965). Reflex effects of slow bladder filling on the blood pressure in cats. *Q. Jl exp. Physiol.* **50**, 263–270.