Reflex Responses of Neurons in the Inferior Mesenteric Ganglion to Mechanical Stimulation of the Colon, Rectum, Anal Canal, and Urinary Bladder in the Dog

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Abstract  Unitary discharges were recorded from the inferior mesenteric ganglion of decerebrate dogs. Eighty-one units were identified as sympathetic postganglionic neurons innervating the colon and rectum by collision test performed by stimulation of the lumbar colonic nerve. Discharges of four units were enhanced simultaneously with an increased outflow of the renal nerve by pinching a toe. Thus, those units were regarded as vasoconstrictors of colonic blood vessels. Sixty-five units whose discharges were depressed or not affected by the pinching were regarded as neurons innervating colonic smooth muscle or mucosa (colonic units). Discharges were enhanced in the majority of the colonic units by colonic, rectal, and vesical distension, and mechanical stimulation of the anal canal, while discharges were depressed in a few units by rectal and vesical distension, and the anal canal stimulation. The number and percentage of the depressed units increased not only after cutting the hypogastric nerves and descending branches of the lumbar colonic nerve but also after transection of the caudal pons. The reflex depressions disappeared after transection at the bulbospinal junction, but the reflex enhancements remained. These results indicate that the colonic units are enhanced through a spinal reflex by the inflows from the distal colon, rectum, anal canal, and urinary bladder through the lumbar colonic, hypogastric, pelvic, and pudendal nerves, while a few are inhibited through a supraspinal reflex by inflows through the pelvic and pudendal nerves.

Key words: inferior mesenteric ganglion, autonomic reflex, sympathetic postganglionic neuron, colon, defecation.
Recently, reflex responses of sympathetic preganglionic fibers in the lumbar splanchnic nerves to distension of the pelvic organs were studied in anesthetized cats (BAHR et al., 1986a, b, c; BARTEL et al., 1986), but it remains uncertain whether the fibers innervate the colon or the urinary bladder.

On the other hand, reflex responses of the sympathetic postganglionic neurons, which are known to innervate the colon and rectum, have been studied in vivo in multi-unit discharges of the lumbar colonic nerve of cats (DE CROAT and KRIER, 1979), guinea pigs (TAKAKI et al., 1980, 1983, 1985), and dogs (OKADA, 1984; FUKAI, 1986), as well as in vitro in discharges of the inferior mesenteric ganglion cells of guinea pigs (CROWCROFT et al., 1971; SZURSZEWSKI and WEEMS, 1976). These works consistently showed that the outflow of the lumbar colonic nerve is enhanced by distension of the colon, but yielded disparate findings in vivo during defecation. DE CROAT and KRIER (1979) did not observe any change in the outflow during defecatory contraction of the rectum in cats. TAKAKI et al. (1985) reported that the outflow was depressed by stimulation of the pelvic afferent fibers from the rectum in guinea pigs and that the depression caused defecatory contraction of the rectum. On the contrary, OKADA (1984) and FUKAI (1986) observed in dogs that an increase of the outflow and a defecatory contraction of the rectum were simultaneously elicited by mechanical stimulation of the anal mucosa.

Thus, we aimed in this work to reexamine reflex responses of the outflow to mechanical stimuli of the colon, rectum, anal canal, and urinary bladder using microelectrodes to extracellularly record unitary discharges of inferior mesenteric ganglion cells innervating the colon and rectum through the lumbar colonic nerve.

MATERIALS AND METHODS

This study was performed in 23 dogs, each weighing 5–10 kg. All dogs were decerebrated precocullarly under anesthesia induced with an intravenous injection of 15 mg/kg of thiopental sodium and maintained with an injection of the same dose given just before the decerebration.

The left renal, pelvic, and lumbar splanchnic nerves, bilateral hypogastric nerves, and lumbar colonic nerve were exposed retroperitoneally by an incision along the membranous ligaments of the external and internal abdominal oblique muscles, the inguinal ligament, and the prepubic tendon.

The colon was ligated about 3 cm anal to the middle colic artery; then, balloons were inserted into the distal colon and the rectum through an incision made in the colonic wall just anal to the ligation (R5 and R6 in Fig. 1). The colon was ligated tightly between both balloons at the level of the inferior mesenteric artery to block conduction of action potentials of colonic smooth muscles and myenteric nervous elements between the segments. Another balloon was inserted through a small incision in the vesical wall where the median umbilical ligament is attached. These balloons were used to record intraluminal pressure and to distend the organs.

A branch of the renal nerve and a postganglionic rectal branch of the pelvic
nerve were isolated, and their centrifugal discharges were recorded with bipolar platinum wire electrodes. The branches of the lumbar colonic nerve ascending along the left colic artery were cut at the level of the oral colonic ligation to prevent the effects brought about on lumbar sympathetic outflow and colonic motility by vagal

Fig. 1. Schema of experimental set up. R1, glass microelectrode and indifferent silver plate electrode used to record unitary discharges of inferior mesenteric ganglion cells. R2 and R3, platinum wire electrodes used to record outflow of the renal nerve and a postganglionic rectal branch of the pelvic nerve. R4, R5, and R6, balloon and vinyl tube used to record intraluminal pressure of the distal colon, rectum, and urinary bladder. S, platinum wire electrode used to stimulate the lumbar colonic nerve for collision tests of unitary discharges of inferior mesenteric ganglion cells.
and splanchnic afferent and efferent fibers. All descending branches of the lumbar colonic nerve which innervate the rectum were isolated at the level of the anal ligation so that they could be cut during the experiment. Similar procedures were performed on the hypogastric nerves. The inferior mesenteric artery was separated from the lumbar colonic nerve and cut just peripheral to the inferior mesenteric ganglion. Then, the artery was pulled out centripetally from the ganglion taking care to preserve the two small arterial branches to the ganglion.

The ganglion was pinned on a small wooden board (8 × 10 × 3 mm) which was attached to the end of a steel rod (20-mm diameter, 200-mm length) at an angle of 120°. The rod was clamped to another rod (30-mm diameter) erected on the steel base used for fixation of the dog. The peripheral connective tissue of the ganglion was gently removed to facilitate easy insertion of the recording electrodes.

Micropipettes (2–3 μm in tip diameter) filled with a saturated water solution of sodium citrate were used to record extracellular unitary discharges of the ganglion cell. To identify the inferior mesenteric ganglion cells innervating the colon and rectum, a collision test was performed as described in our previous work (FUKUDA et al., 1981) by stimulation of the lumbar colonic nerve with a bipolar platinum wire electrode (S in Fig. 1). Responses to distension of the colon, rectum, and urinary bladder, to mechanical stimulation of the anal mucosa, and to pinching of a toe with hemostatic forceps (noxious stimulation) were examined in the units which were confirmed to send axons to the colon. The anal mucosa was stimulated by manual rotation of an acrylic resin rod 12 mm in diameter, which was inserted into the anal canal.

Dogs were paralyzed with intravenous gallamine triethiodide (2 mg/kg), and artificially ventilated through a tracheal cannula at a rate of 15 to 25 strokes/min and a tidal volume of 150 to 250 ml. Arterial blood pressure was monitored through a cannula connected to the right femoral artery. The body temperature was maintained at about 36°C with the heat generated by two 100-W tungsten lamps.

RESULTS

Discharge frequency and conduction velocity of postganglionic sympathetic units

The histogram in Fig. 2A shows conduction velocities of the axons, which were calculated from collision times. The mean velocity of 81 axons was 0.65 ± 0.24 m/s (mean ± S.D.).

Frequencies of spontaneous discharges of the units are shown in Fig. 2B and C. The mean frequency of 2.1 ± 1.5 imp./s (57 units) decreased to 1.3 ± 1.2 imp./s (31 units) after cutting the hypogastric nerves and descending branches of the lumbar colonic nerve which innervate the rectum.

Classification of unit types

Discharges of sympathetic vasoconstrictor fibers in the renal nerve as well as arterial blood pressure are increased by noxious stimulation, while sympathetic...
Fig. 2. Conduction velocities of the axons of the inferior mesenteric ganglion cells (A) and discharging frequencies of the cells before (B) and after (C) cutting the hypogastric nerves and descending branches of the lumbar colonic nerve.
outflows to the stomach of decerebrate dogs and to the jejunum of anesthetized rats are suppressed, respectively, by ocular compression, a pain-causing stimulus in man (Furukawa and Okada, 1983), and by pinching of the paws (Koizumi et al., 1980). Since these observations show that sympathetic fibers innervating the gastrointestinal tract and those innervating the blood vessels respond differently to noxious stimulation of certain parts of the body, we pinched a toe to differentiate vasoconstrictor units in the inferior mesenteric ganglion from the units innervating colonic smooth muscles or mucosa (colonic units).

The vasoconstrictor unit. In all dogs, pinching a toe caused a transient increase followed by a decrease in the outflow of the renal nerve, as well as a subsequent transient increase in blood pressure. Responses to the noxious stimulation were examined in 69 units of the inferior mesenteric ganglion. Discharges

Fig. 3. Reflex responses of a vasoconstrictor unit. From top to bottom the traces show frequency histograms of outflow of a branch of the renal nerve, frequency histograms of unitary discharges of inferior mesenteric ganglion cells, rectangular pulses representing the unitary discharges, intraluminal pressure (A, B, and C, the urinary bladder; D and E, the rectum; F, the distal colon), and blood pressure. A, a toe of the right hind foot was pinched during the periods indicated by horizontal bars. B, the perineal skin was pinched. C, central cut-ends of vesical branches of the left pelvic nerve were stimulated. D, the rectum was distended. E, the anal canal was stimulated mechanically. F, the distal colon was distended. This explanation applies to the following figures.
Table 1. Reflex responses in unitary discharges recorded from the inferior mesenteric ganglion.

I. The colonic units

A. Reflex responses before cutting the hypogastric nerves and descending branches of the lumbar colonic nerve

<table>
<thead>
<tr>
<th></th>
<th>Distension of distal colon</th>
<th>Distension of rectum</th>
<th>Stimulation of anal canal</th>
<th>Distension of urinary bladder</th>
<th>Pinching of a toe</th>
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<tr>
<td>No.</td>
<td>31 7 0</td>
<td>22 16 1</td>
<td>20 14 3</td>
<td>26 10 0</td>
<td>0 17 27</td>
</tr>
<tr>
<td>%</td>
<td>82 18 0</td>
<td>56 41 3</td>
<td>54 38 8</td>
<td>72 28 0</td>
<td>0 39 61</td>
</tr>
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B. Responses after cutting both nerves

<table>
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<tr>
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<tr>
<td></td>
<td>23</td>
<td>92</td>
<td>2</td>
<td>23</td>
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<td></td>
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<td>8</td>
<td>13</td>
<td>62</td>
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<td></td>
<td>3</td>
<td>8</td>
<td>3</td>
<td>14</td>
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II. The vasoconstrictor units

| No.            | 4    | 0    | 0 | 0    | 2    | 2    | 0 | 1    | 2    | 1 | 4    | 0    | 0 | 0 |

Numbers (No.) and percentages (%) of units whose discharges were enhanced (↑), uninfluenced (→), and depressed (↓) by the stimulation indicated are shown.
were enhanced in 4 units by the noxious stimulation simultaneously with a reflex increase in the outflow of the renal nerve (Fig. 3A). Similar enhancement was also elicited by pinching the skin of the perineum in 2 units tested (Fig. 3B). Discharges were enhanced in all 4 units by distal colonic distension, in 2 units by anal canal stimulation and in 1 unit by vesical distension or contraction (Table 1, II). These reflex enhancements due to visceral stimulation were usually small as shown in Fig. 3C, F (compare with Fig. 4A, D), but were always accompanied by a reflex increase in the outflow of the renal nerve and in the blood pressure.

Three out of the 4 units discharged synchronously with the rhythm of artificial ventilation, and the remaining unit fired with the cardiac rhythm.

Fig. 4. Reflex responses of the colonic unit. F, G, H, and I, responses at 6, 31, 39, and 46 min after cutting the hypogastric nerves, respectively. J, K, L, and M, responses at 20, 24, 30, and 54 min after cutting descending branches of the lumbar colonic nerve, respectively. N, a and b, photographs of discharges of the units taken during the periods indicated by a and b in J, respectively.

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These results suggest that the 4 units are the vasoconstrictor neurons innervating the colonic blood vessel.

The colonic unit. Responses of 65 out of 69 units to pinching a toe differed from the response in outflow of the renal nerve. Discharges were depressed in 33 units by the noxious stimulation but not affected in 32 units. No rhythmic changes corresponding to cardiac cycles or artificial ventilation were observed in the discharges of the 65 units.

These results suggest that the 65 units innervate the colonic smooth muscle or mucosa.

Reflex responses of the colonic units

Reflex responses of 44 colonic units to distal colonic, rectal, and vesical distension, and anal canal stimulation were examined before cutting the hypogastric nerves and descending branches of the lumbar colonic nerve. Discharges were enhanced in the majority of the units by these stimuli (Fig. 4A, B, and D, and Table

![Graph showing reflex responses of colonic units](image)

Fig. 5. Frequencies of basal discharges and maximum discharges of the colonic units during reflex responses to distension of the distal colon (A), the rectum (B), and the urinary bladder (D), and to anal canal stimulation (C). Vertical bars, mean frequency ± S.D. (impulses/s). The means of the ratios of maximum frequency/basal frequency in each unit are shown.
The responses to rectal distension and anal canal stimulation were observed in 31 out of the 44 units simultaneously with the reflex responses of a rectal branch of the pelvic nerve. Discharges were enhanced in 17 and 18 out of the 31 units by rectal distension and anal canal stimulation, respectively, while depressed in 1 and 2 units. The enhancements of all but 3 units as well as the depressions in all the units were accompanied by a reflex increase in the outflow of the pelvic rectal branch (Fig. 4B).

Figure 5 shows the maximum discharging frequencies (2–24 imp./s) which were attained in colonic units during distal colonic, rectal, and vesical distension of up to 70–100 mmHg in pressure, and during anal canal stimulation. The ratios of the maximum frequency of each unit to its basal frequency did not differ significantly regardless of the organ stimulated, except that the ratios in the responses to rectal distension were significantly (p < 0.05) larger than those in the responses to anal canal stimulation.

Threshold pressure for reflex enhancements of discharges of the colonic units by distal colonic, rectal, and vesical distension are shown in Fig. 6. The threshold pressures ranged from 5 to 70 mmHg, and the values did not differ significantly regardless of the organ distended.

**Effects of cutting the hypogastric nerves and descending branches of the lumbar colonic nerve on reflex responses of the colonic units**

To ascertain how the afferent fibers in the hypogastric nerve and descending branches of the colonic nerve, and the fibers in the pelvic and pudendal nerves contribute to reflex responses of the colonic units, effects of cutting the hypogastric nerves and the branches of the lumbar colonic nerve were observed in 7 units. The reflex enhancement evoked in 3 units by rectal distension (Fig. 7), in 2 units by vesical distension, and in 1 unit by anal canal stimulation disappeared after cutting the nerves, but the other responses did not change (Fig. 4). In an additional 19 units,
reflex responses to these stimuli were examined only after the nerves were cut. Responses of these units are shown in Table 1, IB. The percentages of the units enhanced by rectal and vesical distension and anal canal stimulation decreased after the cutting, but the percentages of the units depressed by these stimuli increased. However, the percentage of the units enhanced by distal colonic distension did not change significantly.

After cutting the nerves and branches, responses of 24 units to rectal distension and anal canal stimulation were observed simultaneously with the reflex responses of a rectal branch of the pelvic nerve. Five and 7 out of the 24 units were enhanced by rectal distension and anal canal stimulation, respectively, with a simultaneous increase in the outflow of the pelvic rectal branch, while 2 units each were depressed.

These results show that colonic units are under the control of both 1) the enhancing reflexes elicited by the inflows from the distal colon, rectum, anal canal, and urinary bladder through the lumbar colonic, hypogastric, pelvic, and pudendal nerves, and 2) the depressing reflexes elicited by the inflows from these organs (except the distal colon) through the pelvic and pudendal nerves.
Correlation between reflex responses of the colonic unit to rectal and vesical distension

Responses to distension of both the rectum and urinary bladder were examined in 35 units each before cutting the hypogastric nerves and descending branches of the lumbar colonic nerve. Discharges were enhanced in the majority of the units by distension of either organ, but were not influenced in 10 units. In 6 units, the response to rectal distension differed from that to vesical distension: the discharges were enhanced in all 6 units by vesical distension, but were not affected in 5 units, and depressed in 1 unit by rectal distension.

After cutting both nerves, responses of each of the 22 units to distension of either organ were observed. Ten units were not enhanced by either distension: discharges were not affected in 8 units by either distension, were depressed by vesical distension but not affected by rectal distension in 1 unit, and were depressed by rectal distension but not affected by vesical distension in one other unit. Three units

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Fig. 8. A: positions of transections of the neuraxis are shown by horizontal bars. i.c., inferior colliculus; c.p., cerebellar peduncle; Cl, dorsal root of the first cervical nerve. B: effects of the transections on reflex responses of the colonic units. Numerals, numbers of the units showing the responses indicated by ↑ (enhancement), → (no effect), and ↓ (depression). Each unit showing the change in response indicated by an oblique arrow is represented by one filled circle.
were enhanced by either distension, while responses to vesical and rectal distension differed from each other in 9 units: discharges were enhanced in 7 units by vesical distension but not by rectal distension, and enhanced in 2 units by rectal distension but not affected by vesical distension.

**Effects of transection of the neuraxis on reflex responses of the colonic unit**

The neuraxis was transected at the caudal pontine level and at the bulbospinal junction to define the brain area mediating the reflex enhancement and depression of the colonic units resulting from distal colonic, rectal, and vesical distensions, and anal canal stimulation (Fig. 8A). The unit shown in Fig. 9 is the same unit shown in Fig. 4. The reflex enhancement due to rectal distension disappeared after caudal pontine transection (Fig. 9B), but the enhancements due to distal colonic and vesical distension remained after this transection (Fig. 9A, C), as well as after transection at the bulbospinal junction (Fig. 9E). Moreover, the enhancement due to rectal distension reappeared and that due to anal canal stimulation appeared.

![Diagram of reflex responses](image)

**Fig. 9.** Effects of transections of the neuraxis on reflex responses of the same units of Fig. 4. A, B, C, and D, responses elicited 10, 15, 23, and 42 min after transection of the caudal pons, respectively. E, a continuous record showing responses from 1.2 to 6 min after transection of the bulbospinal junction.
for the first time after transection at the bulbospinal junction (Fig. 9E).

Another example is shown in Fig. 7. This unit showed no clear responses to rectal distension and to anal canal stimulation after cutting the hypogastric nerves and descending branches of the lumbar colonic nerve (Fig. 7D, E), but its discharges were depressed by both stimuli after caudal pontine transection (Fig. 7F, G). Moreover, both depressions changed to enhancements after transection at the bulbospinal junction (Fig. 7H, I).

Effects of both transections on reflex responses of 6 units are summarized in Fig. 8B. The enhancement resulting from rectal distension disappeared in 2 units after caudal pontine transection, and that due to anal canal stimulation changed to a depression in 1 unit. After the transection, rectal distension and anal canal stimulation resulted in depression of reflex responses in 2 units which had not shown any responses before the transection. After subsequent transection at the bulbospinal junction, the depression by rectal distension changed to an enhancement in 3 units. Moreover, an enhancement was newly elicited by rectal and vesical distension, and anal canal stimulation in 1 unit each. The disappearance of a response in 2 or more units, and the appearance of a novel response or reversal of a response from enhancement to depression or vice versa in one or more units indicate that the changes are a consequence of the transection and are not chance occurrences. Such changes are shown by thick arrows in Fig. 8B.

DISCUSSION

The present work is the first one where unitary discharges were recorded in vivo from the inferior mesenteric ganglion. The discharge frequency, conduction velocity, and reflex responses were determined in the postganglionic sympathetic neurons which innervate the colonic smooth muscle or mucosa (colonic units).

The mean conduction velocity (0.65 ± 0.24 m/s) determined in this study was slightly faster than the modal conduction velocity (0.3–0.4 m/s) measured in vitro in dogs by King and Szurszewski (1984). The mean frequency (2.1 ± 1.5 imp./s) of the basal discharges of the colonic units decreased to 1.3 ± 1.2 imp./s after cutting the hypogastric nerves and descending branches of the lumbar colonic nerve. Even the decreased frequency was higher than that (0.8 ± 0.7 imp./s) of unitary discharges of the lumbar splanchnic nerves measured by Bahr et al. (1986c) in anesthetized cats.

Reflex responses of the colonic units.

Reflex enhancements: In the present experiments, an enhancement of unitary discharges was observed in the responses of all but 4 colonic units to rectal distension and anal canal stimulation. This result agrees well with changes in multiunit discharges of the lumbar colonic nerve of dogs (Okada, 1984; Fukai, 1986) and of guinea pigs (Takahashi et al., 1980). Moreover, the reflex enhancement of the colonic units due to either stimulus was usually accompanied by a reflex increase in the outflow of rectal branches of the pelvic nerve. Therefore, it may be concluded
that the sympathetic outflow to the colon and rectum increases during defecation. Accordingly, smooth muscles of the colon and rectum seem to be influenced during defecation not only by increased excitatory effects of sacral parasympathetic outflow (Okada et al., 1975, 1976, 1977; De Groat and Krier, 1978; Fukuda et al., 1981) but also by increased inhibitory effects of lumbar sympathetic outflow. However, a defecatory contraction is always brought about on the rectum as a result of the sum of excitatory and inhibitory effects, while a depression of motility is induced on the proximal colon (as observed in dogs by Lawson and Tempelton (1931) and Okada et al. (1977)), probably due to a stronger excitatory effect on muscles of the rectum than on those of the proximal colon (Fukai and Fukuda, 1984).

Reflex enhancements of the lumbar sympathetic outflow to the colon and rectum were also induced by stimulation of viscera other than the rectum and anal canal. Discharges were enhanced in the majority of the colonic units by distal colonic and vesical distension in the present experiment as observed in multi-unit discharges of the lumbar colonic nerve during distension of the proximal colon of dogs (Fukai, 1986) and of cats (De Groat and Krier, 1979), and during vesical distension in cats (De Groat and Lalley, 1972). Thus, it may be concluded that the sympathetic outflow is enhanced by colonic and vesical distension. The enhancements seem to be consistent with reflex inhibition brought about on colonic motility by colonic (Semba, 1955; Ohashi, 1969) and vesical distension (Hayasi, 1959).

The results from the experiment in which the hypogastric nerves and descending branches of the lumbar colonic nerve were cut show that the reflex enhancement of the colonic units due to distal colonic distension was mediated by the afferent fibers in the lumbar colonic nerves, while enhancement due to rectal and vesical distension and anal canal stimulation was related to the fibers in the lumbar colonic, hypogastric, pelvic, and pudendal nerves. The enhancement remained after transection of the bulbospinal junction. Thus, it may be concluded that the enhancement due to pelvic and pudendal nerve afferents are mediated by a spinal reflex, since the afferent fibers ascend directly to the sacral spinal cord. It cannot, however, be determined from the results whether either or both of the spinal reflex and the reflex which is completed at the inferior mesenteric ganglion level (Crowcroft et al., 1971; Szurszewski and Weems, 1976) mediate the enhancement elicited by activity of afferent fibers in the hypogastric and lumbar colonic nerves.

On the other hand, Fukai (1986) showed in dogs that outflow of the lumbar colonic nerve and its reflex increase caused by colonic distension disappeared after destruction of the lumbar segment of the spinal cord or its anesthesia with xylocaine. Moreover, De Groat and Krier (1979) observed in the nervous outflow of cats that the reflex enhancement resulting from mechanical stimulation of the proximal colon was blocked by transection of the lumbar dorsal roots. Therefore, the enhancement of the sympathetic outflow to the colon and rectum elicited by activity of colonic afferent fibers in the lumbar colonic and hypogastric nerves seems to be mediated mainly by a spinal reflex at least in dogs and cats as is the reflex enhancement.
induced by pelvic and pudendal nerve afferents. Nevertheless, a colo-colonic inhibitory reflex mediated by the prevertebral ganglia is supported by evidence from in vitro experiments in guinea pigs (Crowcroft et al., 1971; Szurszewski and Weems, 1976; Kreulen and Szurszewski, 1979).

**Reflex depression:** The discharges in a few of the colonic units were depressed by rectal distension and anal canal stimulation. The number as well as the percentage of colonic units showing the depression increased not only after cutting the hypogastric nerves and descending branches of the lumbar colonic nerve but also after transecting the caudal pons. On the contrary, the depression was blocked or changed to an enhancement by transection of the bulbospinal junction. Thus, it may be concluded that some colonic units which are enhanced through a spinal reflex are depressed by activity of the afferent fibers in the pelvic and pudendal nerves through a supraspinal reflex mediated by bulbar neurons. This conclusion is supported in part by the results showing that inflows from the urinary bladder and vagina through the pelvic and pudendal nerves project onto some bulbar neurons (Kuru, 1956; Rose and Sutin, 1973; Hornby and Rose, 1976). Furthermore, the results of the transection of the caudal pons (Fig. 8B) suggests that some neurons in the pons and/or midbrain suppress the bulbar neurons which mediate the reflex depression of the colonic units.

Furthermore, Takaki et al. (1985) observed in guinea pigs, in which all nerves innervating the colon were cut except the lumbar colonic nerve, that a depression in the outflow of the lumbar colonic nerve was elicited simultaneously with a rectal contraction by stimulation of rectal afferent fibers in the pelvic nerve. From these results, they concluded that the depression in the sympathetic outflow causes a defecatory contraction of the rectum. The reflex depression of the colonic units in the present experiment may correspond to the depression of the outflow of the lumbar colonic nerve of guinea pigs. However, we did not observe the reflex depression in so many colonic units so as to expect that the depression elicits a rectal contraction. The reason for the difference between their and our observations has not been clarified.

Barzel et al. (1986) reported that the unitary discharges on the lumbar splanchnic nerve were depressed by distension of the distal colon even after transection of the spinal cord at the lower thoracic level in cats. Their results contradict the present result in dogs and the results obtained by Takaki et al. (1980, 1983, 1985) in guinea pigs. Therefore, it seems likely that the preganglionic sympathetic units in the lumbar splanchnic nerves may innervate organs other than the colon and rectum through the hypogastric nerve. Alternatively, the possibility that the contradiction is due to a species difference cannot be ruled out.

Correlation between reflex responses of the colonic units to rectal and vesical distension. Recently, Bahr et al. (1986a) classified lumbar sympathetic pre-ganglionic fibers onto MR1 and MR2 neurons according to their response to vesical and rectal distensions. Namely, MR1 neurons are excited by vesical distension but inhibited or not influenced by rectal distension, and, conversely, MR2 neurons are
excited by rectal distension but not by vesical distension. From these results, they suggested that MR1 neurons inhibit motility of the colon and rectum during vesical voiding contraction and MR2 neurons inhibit detrusor muscles during rectal defecatory contraction.

The colonic units which innervate the colon and rectum are MR1 neurons according to the suggestion of Bahr et al. (1986a), but contrary to their suggestion, the discharges in the majority of the colonic units were enhanced by both rectal and vesical distension. Our result suggests that the sympathetic fibers innervating the colon and rectum cannot be distinguished from the fibers innervating the bladder by their response types to rectal and vesical distension.

The vasconstrictor units. Rhythmic changes synchronous with cardiac and/or respiratory cycles were found in 10 of 63 discharges of bundles isolated from the lumbar colonic nerve of cats (De Groat and Krier, 1979), and in 49 of 170 in unitary discharges of the lumbar splanchnic nerves (Bahr et al., 1986b). These incidences are higher than that (4/69) of vasoconstrictor units in the present experiment. On the other hand, Baron et al. (1985) showed that some sympathetic postganglionic cells in the lumbar paravertebral ganglia send their axons along the lumbar colonic nerve. Therefore, the lesser incidence in the present experiment suggests that these paravertebral ganglion cells are vasoconstrictors, since the axons of the paravertebral ganglion cells may be C fibers, and accordingly their discharges might not be recorded by our electrodes of 2–3 μm in tip diameter.

During visceral stimulation, discharges of some vasoconstrictor units (Table 1, II) increased while those of others decreased in parallel with the responses of the renal nerve, although the changes were usually smaller than those shown by the colonic units. This result is consistent with the observations of Bahr et al. (1986b) concerning the responses of single fibers of the lumbar splanchnic nerve, which discharged with cardiac and/or respiratory rhythms.

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