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Abstract

The role of the lumbar sympathetic nerves and supraspinal mechanism in the defecation reflex was investigated in 30 adult cats and 6 kittens. One or two propulsive contractions, whose mean pressure evoked was more than about 90 cmH2O (adult cats) and 50 cmH2O (kittens), were induced in the rectum of all animals by rectal distension. These propulsive contractions could be generated at the descending and the transverse colons. The removal of the supraspinal influence by spinal transection at T13 or removal of pelvic afferents to the supraspinal center by spinal transection at L abolished the propulsive contractions. Successive lumbar sympathectomy restored the contractions. Lumbar sympathectomy and the successive removal of the supraspinal influence did not affect the propulsive contractions. In both cases, the final exclusion of the sacral segments by pithing of the spinal cord abolished the propulsive contractions. These results suggest that the sacral excitatory reflex mediated via pelvic nerves and the lumbar inhibitory reflex mediated via lumbar sympathetic nerves can function during rectal distension in spinal cats and that the lumbar inhibitory reflex is suppressed by the supraspinal sympathetic inhibitory reflex activated by pelvic afferents in intact cats, as in guinea pigs, resulting in propulsive contractions.

KEYWORDS: lumbar sympathectomy, defecation reflex, cats, rectal distension

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Functional Role of Lumbar Sympathetic Nerves and Supraspinal Mechanism in the Defecation Reflex of the Cat

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The role of the lumbar sympathetic nerves and supraspinal mechanism in the defecation reflex was investigated in 30 adult cats and 6 kittens. One or two propulsive contractions, whose mean pressure evoked was more than about 90 cmH_2O (adult cats) and 50 cmH_2O (kittens), were induced in the rectum of all animals by rectal distension. These propulsive contractions could be generated at the descending and the transverse colons. The removal of the supraspinal influence by spinal transection at T_{13} or removal of pelvic afferents to the supraspinal center by spinal transection at L_{5-6} abolished the propulsive contractions. Successive lumbar sympathectomy restored the contractions. Lumbar sympathectomy and the successive removal of the supraspinal influence did not affect the propulsive contractions. In both cases, the final exclusion of the sacral segments by pithing of the spinal cord abolished the propulsive contractions. These results suggest that the sacral excitatory reflex mediated via pelvic nerves and the lumbar inhibitory reflex mediated via lumbar sympathetic nerves can function during rectal distension in spinal cats and that the lumbar inhibitory reflex is suppressed by the supraspinal sympathetic inhibitory reflex activated by pelvic afferents in intact cats, as in guinea pigs, resulting in propulsive contractions.

Key words : lumbar sympathectomy, defecation reflex, cats, rectal distension

We have fully investigated the role of lumbar sympathetic nerves (especially lumbar colonic nerves) in the defecation reflex of the guinea pig (1-4). Although the manner in which guinea pigs defecate is quite different from that of other mammals, *e. g.*, humans, monkeys, dogs and cats, we revealed that a descending nerve pathway which inhibits the lumbar sympathetic component (mediated via lumbar colonic nerves) of the recto-rectal reflex may originate in the pons. The sensory limb of this supraspinal sympathetic inhibitory reflex arc is represented by afferent fibers in pelvic nerves.

The manner of defecation in cats appears to be similar to that in humans, *i. e.*, the cat can maintain feces in the transverse and distal colons and defecate once or twice a day. Garry (5) found that defecation could be elicited with greater ease after division of the lumbar sympathetic outflow. De Groat *et al.* (6) have reported that the supraspinal reflex center does not function on the outflow of lumbar sympathetic nerves in the cat. In contrast, Bahr *et al.* (7, 8) and Bartel *et al.* (9) have recently reported that, in cats, most of the motility-regulating preganglionic neurons projecting in the lumbar splanchnic nerves exhibited three different reflex patterns upon colon distension and that those reflexes use spinal pathways, which are probably controlled by descending inhibitory and excitatory spinal systems from the supraspinal neuraxis. In the present study, we examined the role of lumbar sympathetic nerves in the defecation reflex of cats in order to compare it with the role of these nerves in the defecation reflex of guinea pigs.

Materials and Methods

Thirty adult cats and 6 kittens of either sex were used. They were anesthetized with ketamine (5-50 mg/kg, i. m.) alone or with additional chloralose (30-50 mg/kg, i. v.) and immobilized with gallamine triethiodide (0.05-0.1 mg/kg, i. v.). The cats were artificially ventilated with the respiratory rate and tidal volume adjusted to keep arterial blood gases within normal limits (P_{CO_2}, 35-40 mmHg; P_{O_2} 80-100 mmHg; pH, 7.2-7.5). To maintain the blood pressure in the appropriate range (higher than 100 mmHg) throughout the experiment, lactate-Ringer solution containing 0.02 % gallamine triethiodide was administered at 6-7 ml/h into the femoral vein. In some animals, the blood pressure of the common carotid artery was monitored. The abdomen was opened through a midline incision. The contents were found in the large intestine as described by Hedlund *et al.*(10), and these contents were gently removed by infusion of warm Tyrode solution (37°C) from the anus. A 2-cm (volume, 3 ml) or 6-cm-long (volume, 45 ml) balloon was inserted into the rectum, 4-7 cm oral to the anus. This balloon was attached to a stainless steel pipe, which was clamped outside the anus to prevent the evacuation of the balloon (see Fig. 2, B). For kittens, a 2-cm-long balloon was used. The rectum was distended by infusion of 0.9-3 ml (for kittens) and 0.9-40 ml (for adult cats) of warm water (37°C) into the balloon for 5 min at 20-min intervals. The reflex contraction in the rectum induced by the rectal distension (the recto-rectal reflex) was recorded with a pressure transducer. In order to define the generation of the reflex contraction in the large intestine, extraluminal strain gage transducers were sutured on the serosa of the ascending, transverse and descending colons (11) in the direction of the longitudinal and/or circular axis, and then longitudinal and/or circular muscle motility was recorded on a pen-oscillograph via an amplifier (Nihon-Kohden, Tokyo, Japan) in 5 cats. It is well-known that the vesico-vesical reflex contraction is mediated via the pons (12). The disappearance of this reflex after T_{13} transection indicates that the pons is functioning well and that the supraspinal descending pathway is excluded. The vesico-vesical reflex was induced in some cats by infusion of 5 ml warm water into a balloon in the urinary bladder to compare the reflex with the recto-rectal reflex evoked by balloon distension. Lumbar sympathectomy was done by dividing the bilateral hypogastric nerves, colonic nerves, intermesenteric nerves and pre-ganglionic nerves to the inferior mesenteric ganglia.

Results

The rectum was distended stepwise by infusing 5-40 ml of warm water into the 6-cm-long balloon for 5 min at intervals of 20 min. When the basal pressure generated by infusing 25-40 ml of warm water reached 65 to 130 cmH_2O, as shown in Fig. 1, propulsive contractions (the recto-rectal reflex contractions) were evoked in the rectum in all 30 adult cats. The threshold of the basal pressure at which propulsive contractions occurred ranged from 65-100 cmH_2O (Mean ± S.E.: 71.2 ± 10.5 cmH_2O ; n = 4). An example of the measurements of the basal pressure and the propulsive contraction is shown in Fig. 2, A-c. One propulsive contraction was evoked in 22 (73.3%) out of the 30 adult cats, and two contractions were evoked in the remaining 8 animals (26.7%) during 5 min of rectal distension at the threshold or supra-threshold basal pressure. The mean pressure evoked by contractions was 91.3 ± 32.4 cmH_2O (Mean ± S.E.) in the former group (Table 1, I), and 111.6 ± 48.3 (the 1st contraction) and 102.8 ± 34.7 (the 2nd one) in the latter group (Table 1, II). In all 6 kit-

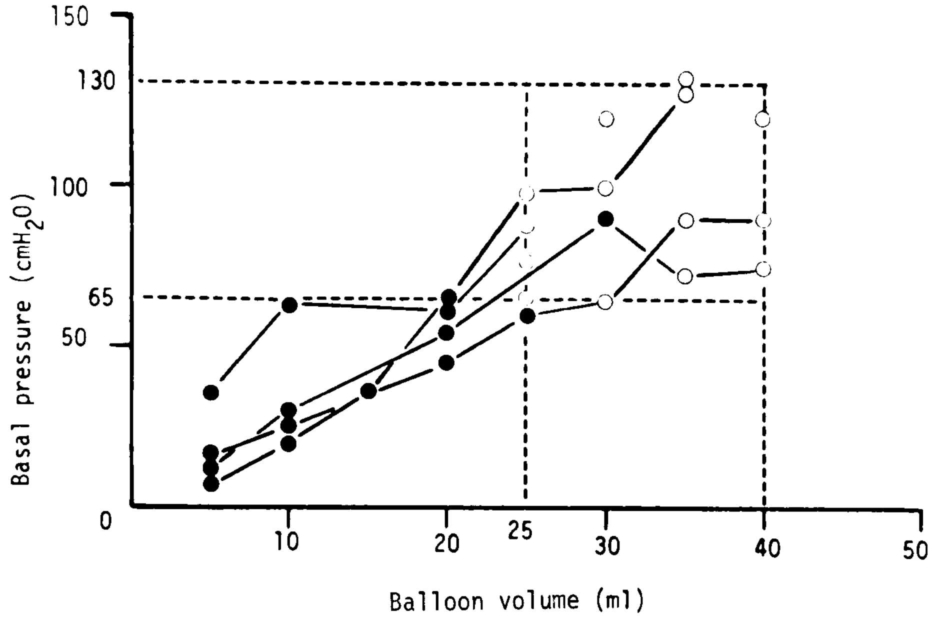

Fig. 1 Threshold of reflex propulsive contraction in the rectum induced by rectal distension in 9 adult cats. Ordinate: the basal pressure (cmH_2O) generated by infusing warm water (37°C) into a 6-cm-long balloon in the rectum. Abscissa: volume (ml) of warm water infused into the balloon. The balloon was distended stepwise by infusing 5-40 ml of warm water for 5 min at 20-min intervals in 4 animals. In another 5 animals, the reflex propulsive contraction was evoked between 65 and 130 cmH_2O of basal pressure by infusing 25-40 ml of water. The threshold ranged from 65-100 cmH_2O. ●, no propulsive contractions evoked; ○, propulsive contractions evoked.

Table 1 Characteristics of propulsive contractions evoked by the recto-rectal reflex in cats[a]

	Group	n[b]	First contraction			Second contraction		
			P (cmH_2O)	D (sec)	L (sec)	P (cmH_2O)	D (sec)	L (sec)
Adult cats	I	22	91.3±32.4	66.8±24.5	163.4±89.2	–	–	–
	II	8	111.6±48.3	47.1±13.6	75.7±24.1	102.8±34.7	55.1±24.1	223.2±52.5
Kittens		6	52.9±19.9	61.0±24.6	111.0±72.1	–	–	–

a: Pressure (P), duration (D) and latency (L) of propulsive contractions were determined. In adult cats, one propulsive contraction was evoked in group I and two in group II.
b: Number of animals.

tens, one propulsive contraction was evoked, and the mean pressure of the contraction was 52.9±19.9 cmH_2O (57.9% of the first group of adult cats, not a statistically significant difference). Neither a difference in the duration nor in the latency of the contraction was found between the adult cats and kittens. The values of the duration and latency varied between individual cats and kittens (Table 1). The propulsive contractions were generated 12-15 cm oral to the anus in the transverse colon, which corresponds to about 65-75% of the total length (17-21.5 cm) of the large intestine, in 4 out of 5 animals examined. In the one remaining animal, the propulsive contraction was not evoked at the transverse colon, but was evoked at the descending colon. In the

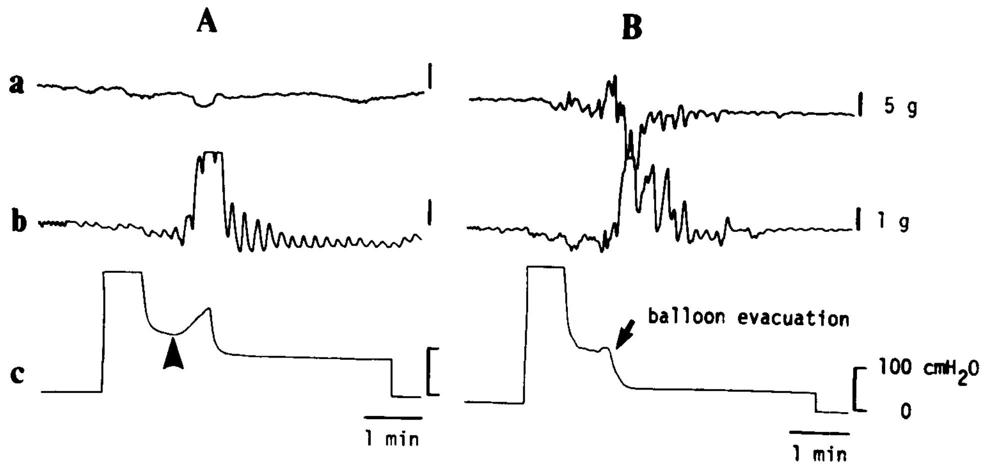

Fig. 2 The reflex propulsive contractions in the large intestine induced by rectal distension. Traces A and B were recorded from two different animals. Forty ml of warm water (37°C) was infused into a 6-cm-long balloon (c in A and B). A, a: circular muscle motility of the ascending colon 18 cm oral to the anus; b: circular muscle motility of the transverse colon 12 cm oral to the anus; c: rectal motility. B, a and b: longitudinal muscle motility of the transverse colon 14 cm (a) and 12 cm (b) oral to the anus; c: rectal motility. The total length of the large intestine was 21.5 cm (A) and 20.5 cm (B). In A-c, the arrowhead (▲) indicates the basal pressure at which a propulsive contraction was evoked. In B-c, the arrow indicates when the balloon in the anus was evacuated by releasing the clamp.

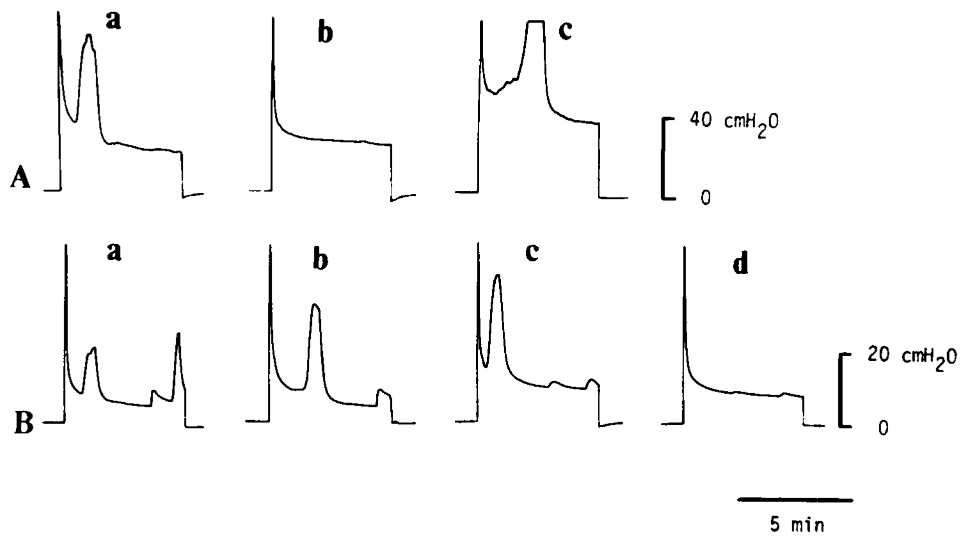

Fig. 3 Effects of exclusion of the reflex pathway on the recto-rectal reflex in kittens. Water, 1.8 ml (A) or 2.5 ml (B), was infused into the balloon. A, a: control; b: 41 min after T_{13} transection to exclude the supraspinal neuraxis; c: 28 min after lumbar sympathectomy. All procedures were done successively. B, a: control; b: 51 min after lumbar sympathectomy; c: 3 h 15 min after T_{13} transection; d: 45 min after pithing lower than L_6 to exclude the sacral parasympathetic segments. All procedures were done successively.

ascending colon, no propulsive contractions were evoked by the rectal distension in four cats except for one, in which the motility of the ascending colon was not recorded. Propulsive contractions in the transverse and descending colons were recorded along both the longitudinal (L) and circular (C) axes of the colon (Fig. 2).

We examined the mechanism of the propulsive recto-rectal reflex contraction evoked by rectal distension in 6 kittens and 15 adult cats. No difference in the mechanism was found between the kittens and adult cats. The contraction was abolished after transection of the spinal cord at the level of the 13th thoracic segment (T_{13}) (Fig. 3, A-b) in 6 animals and reappeared after subsequent lumbar sympathectomy (Fig. 3, A-c) in all 4 animals tested. The restored contraction was abolished after either pithing the spinal cord lower than the level of the 6th lumbar segment (L_6) to exclude the sacral parasympathetic segments in 2 out of 3 animals or injecting atropine (1.0 mg/kg, i.v.) (data not shown) in one out of 3 animals tested. Conversely, the reflex contraction did not change at all in comparison with the control after the lumbar sympathectomy alone (Fig. 3, B-b). Subsequent transection of the spinal cord at T_{13} did not affect the contraction (Fig. 3, B-c) in 7 animals, while the vesico-vesical reflex contraction disappeared in all 4 animals tested. The recto-rectal reflex contraction was abolished after pithing of the spinal cord lower than L_6 (Fig. 3, B-d) in all 5 animals tested. Furthermore, after chemical sympathectomy by application of guanethidine (15 mg/kg, i.v.; Fig. 4-I) (13),

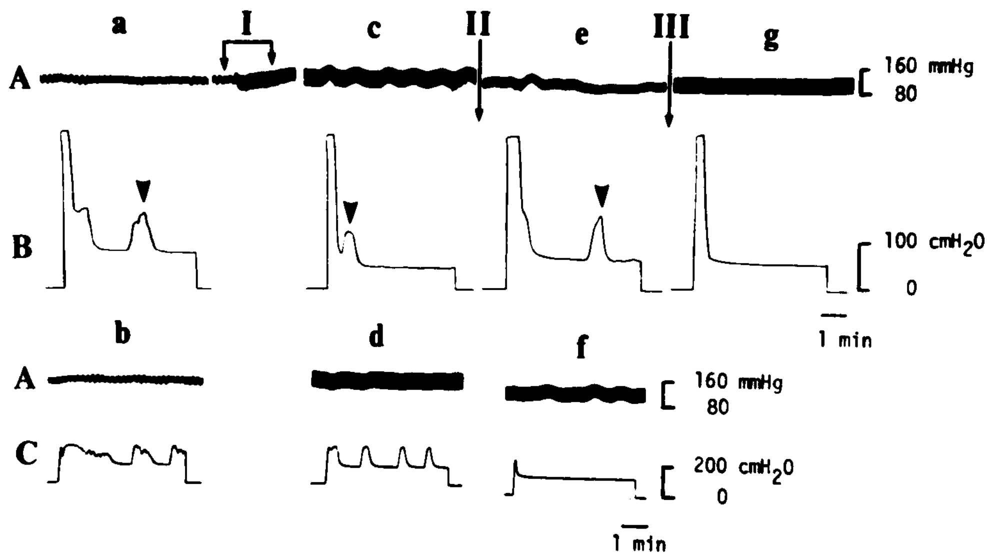

Fig. 4 Effects of guanethidine (15 mg/kg, i.v.; I), T_{13} transection (II) and atropine (0.1 mg/kg, i.v.; III) on the recto-rectal and vesico-vesical reflexes in the same cat. A, systemic blood pressure. B, rectal motility. C, vesical motility. Rectal (infusion volume: 25 in a,c,e and 30 ml in g) and vesical (infusion volume: 4 ml) distension done alternately. Neither guanethidine (A-c, d) nor T_{13} transection (A-e, f) affected the blood pressure. Recto-rectal reflex contraction (▼) was unaffected up to 110 min after guanethidine (B-c) and 20 min after subsequent T_{13} transection (B-e), but was abolished by atropine (B-g). Vesico-vesical reflex contractions were enhanced 120 min after guanethidine (C-d) and abolished by T_{13} transection (C-f).

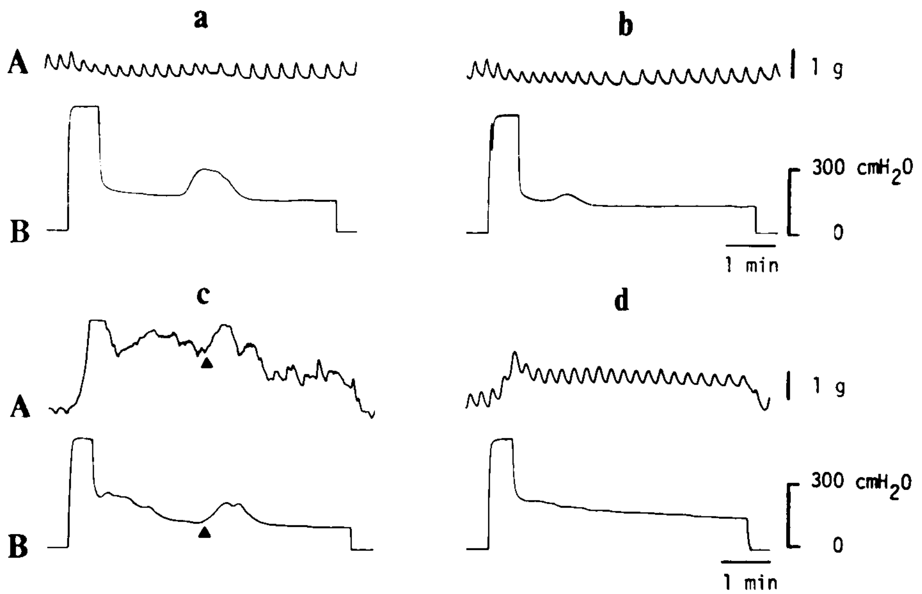

Fig. 5 Effect of exclusion of reflex pathway on the recto-rectal reflex response. A, circular muscle motility at the boundary between the ascending and transverse colons 13 cm oral to the anus. B, rectal motility. Propulsive contraction evoked by infusing 40 ml of water into a 6-cm-long balloon. a, control; b, 94 min after transection between L_5 and L_6 to exclude the ascending pelvic inputs; c, 83 min after lumbar sympathectomy. At the triangles, propulsive contractions were simultaneously recorded in A and B; d, 25 min after pithing lower than L_6 to exclude the sacral segments. In A-c and d, a sustained increase of the basal tone was also observed. All procedures were done successively.

a propulsive reflex contraction comparable to the control contraction was evoked (Fig. 4, B-c). Subsequent transection at T_{13} (Fig. 4-II) did not affect the response (Fig. 4, B-e) in contrast to the vesico-vesical reflex contraction (Fig. 4, C-f), but atropine (0.1-1.0 mg/kg, i.v.; Fig. 4, III) abolished it (Fig. 4, B-g) in 3 animals. To reconfirm the sacral parasympathetic excitatory reflex, the effect of hexamethonium (10 mg/kg, i.v.) was examined in one animal. The propulsive reflex contraction was abolished by application of hexamethonium as predicted, while the blood pressure did not decrease (data not shown). These results suggest possible role of the supraspinal inhibitory reflex center in the lumbar inhibitory outflow. Therefore, the afferent nerve pathway to the supraspinal inhibitory reflex center was examined in 4 cats. The reflex contraction was abolished or substantially reduced by transection between L_5 and L_6 to exclude ascending pelvic inputs to the supraspinal center while leaving the lumbar sympathetic outputs intact (8, 14) (Fig. 5, B-b) in all cats (In guinea pigs, this level corresponds to L_4 and L_5 (15)). Furthermore, after lumbar sympathectomy (Fig. 5, c), the propulsive contraction was evoked by rectal distension in both the boundary between the ascending and transverse colons (13 cm oral to the anus; A) and the rectum (B).

When the rectum was not distended enough to cause a propulsive contraction (subthreshold distension), i,e., short balloon (2 cm long) and small volume of water (0.9 ml), only rhythmic contractions of small amplitude (frequency: 20-23 contractions per 5 min) occurred. These contractions did not change after transection at T_{13} (Fig. 6, A-b), but

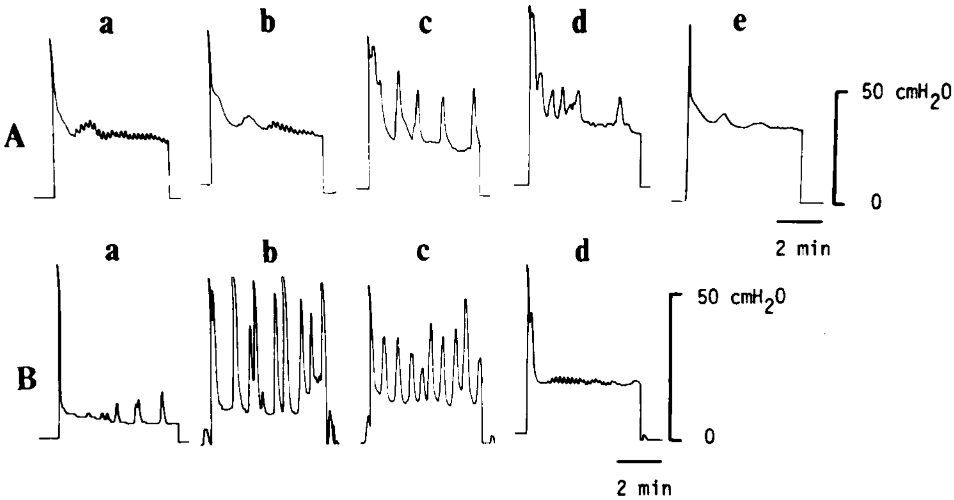

Fig. 6 Effect of exclusion of the reflex pathway on the recto-rectal reflex by infusing 0.9 ml of water into a 2-cm-long balloon in two different adult cats (A and B). A, a: control; b: 63 min after T_{13} transection to exclude the supraspinal neuraxis; c: 38 min after lumbar sympathectomy; d: 31 min after pithing lower than L_1 to exclude the lumbar sympathetic and sacral parasympathetic segments; e: 25 min after atropine (0.1 mg/kg, i.v.). B, a: control; b: 65 min after lumbar sympathectomy; c: preceding pithing between L_1 and L_5 to reconfirm the lumbar sympathectomy and 75 min after T_{13} transection; d: 25 min after pithing lower than L_6 to exclude sacral segments. All procedures were performed successively.

subsequent lumbar sympathectomy produced intensive rhythmic contractions (mean evoked pressure ± S.E.: 23.9 ± 1.7 cmH_2O; n = 5; Fig. 6, A-c). These contractions were remarkably attenuated or abolished by the pithing of the spinal cord lower than L_1 (Fig. 6, A-d) to exclude the lumbar and sacral segments. The remaining contractions were almost completely abolished by atropine (Fig. 6, A-e). Conversely, lumbar sympathectomy performed prior to the pithing enhanced the amplitude of the rhythmic contractions (mean evoked pressure ± S.E.: 37.7 ± 4.2 cmH_2O; n = 9; Fig. 6, B-b), and subsequent transection at T_{13} (and the pithing between L_1 and L_5 to reconfirm the lumbar sympathectomy) slightly decreased the amplitude, but did not affect the frequency of these contractions (Fig. 6, B-c). The pithing of the spinal cord lower than L_6 to exclude the sacral segments abolished the contractions (Fig. 6, B-d), although the rhythmic contractions of small amplitude, as the control (a) in Fig. 6, A, remained. Therefore, it seems that the intrinsic excitatory reflex was evoked by a subthreshold rectal distension.

Discussion

It is well-known that the recto-rectal excitatory reflex evoked by distension is essentially mediated via sacral parasympathetic pathways (16, 17). This mechanism was reconfirmed by the present results that a reflex contraction could be produced after lumbar sympathectomy and spinalization at T_{13}, but was completely abolished by the pithing of the sacral cord. In the present study, lumbar sympathectomy or chemical sympathectomy alone did not affect the recto-rectal reflex propulsive contraction. The removal of the supraspinal influence by spinalization at T_{13} abolished the contraction, and successive lumbar sympathectomy restored the contraction. It was, therefore, assumed that tonic inhibitory outflow through lumbar sympathetic efferents on the rectum and/or reflex inhibition mediated via lumbar sympathetic nerves evoked by rectal distension were suppressed by supraspinal inhibition which is reflexly induced by rectal distension. In the guinea pig, we have shown that the recto-rectal reflex contraction does not change after lumbar sympathectomy alone but is abolished after spinalization at T_{13} and restored after successive lumbar sympathectomy (as shown in the cat in the present study). Tonic activity of lumbar sympathetic post-ganglionic efferents did not change or increased only slightly upon rectal distension in an intact guinea pig, but the activity increased markedly after removal of the supraspinal influence by spinal transection at T_{13} or removal of ascending pelvic afferents by spinal transection at L_4 (1). It has been demonstrated that lumbar sympathetic postganglionic neurons are activated spinally through lumbar sympathetic afferents by distension of the colon (6) and that lumbar sympathetic preganglionic motor neurons were controlled by the supraspinal reflex activated by stimulation of pelvic afferents in cats (7). From these results, it is conceivable that the sacral parasympathetic excitatory reflex, lumbar sympathetic inhibitory reflex, and supraspinal inhibitory reflex on the lumbar sympathetic inhibitory reflex (supraspinal sympathetic inhibitory reflex) are simultaneously produced by rectal distension in the cat as in the guinea pig. Therefore, it is likely that the activity of the lumbar inhibitory reflex but not the tonic activity of lumbar sympathetic efferents is suppressed by the supraspinal sympathetic inhibitory reflex, resulting in the predominance of the sacral parasympathetic excitatory reflex and generation of the propulsive reflex contraction (defecation reflex) in cats as in guinea pigs (1-4).

The subthreshold distension did not evoke propulsive contractions but caused rhythmic contractions of small amplitude in intact and acute spinal cats. The contractions were enhanced by lumbar sympathectomy and abolished by removal of the sacral parasympathetic segments. These results suggest that the subthreshold rectal distension elicited the lumbar sympathetic inhibitory reflex and the sacral excitatory reflex, but did not elicit the supraspinal sympathetic inhibitory reflex. The results also suggest that the threshold to elicit the supraspinal sympathetic inhibitory reflex might be higher than that for the spinal inhibitory reflex. De Groat and Krier (6) have found that the lumbar inhibitory reflexes mediated via lumbar sympathetic neurons (lumbar colonic and hypogastric nerves) were evoked by rapid distension, stretching or pinching of the proximal colon with forceps. The reflexes were also observed in acute spinal cats. Their results coincide with our present results that the subthreshold rectal distension elicited the lumbar sympathetic inhibitory reflex in intact and acute spinal cats. Therefore, the stimulation they used was probably insufficient to evoke the supraspinal sympathetic inhibitory reflex.

The afferent pathway to the supraspinal inhibitory reflex center might be pelvic nerves in cats as is the case in guinea pigs (1, 3, 4), since spinal transection between L_5 and L_6 to exclude ascending pelvic inputs almost abolished the recto-rectal reflex propulsive contraction and since the reflex contraction reappeared after lumbar sympathectomy. The afferent limb of the inhibitory vesico-sympathetic reflex arc in cats, which is supraspinally inhibited by the descending pathway, also exists in the pelvic nerves (18).

The threshold to elicit the reflex contraction ranged from 65 to 100 cmH_2O (Mean± S.E.: 71.2±10.5 cmH_2O; n = 4) in cats, whereas the threshold in guinea pigs ranged from 43 to 69 cmH_2O (1). Moreover, the reflex pattern in cats was quite different in frequency and duration of propulsive contractions from that in guinea pigs (1).

It is conceivable that optimum stimulation of the rectum could evoke both the sacral excitatory reflex via pelvic nerves and the lumbar inhibitory reflex via lumbar sympathetic nerves to act on the defecation reflex, but the supraspinal inhibitory reflex activated by pelvic afferents could function simultaneously to suppress the activity of the lumbar sympathetic inhibitory reflex (supraspinal sympathetic inhibitory reflex). Finally, the propulsive reflex contraction induced by rectal distension (defecation reflex) could occur in the transverse and distal colons as well as in the rectum.

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