Pflügers Arch (1987) 410:296–303

Pflügers Archiv
European Journal of Physiology

Responses of sacral visceral afferents from the lower urinary tract, colon and anus to mechanical stimulation*

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Abstract. The discharge characteristics of sacral visceral afferents supplying the urinary bladder, urethra, colon and anus to mechanical stimuli were analyzed in the anaesthetized cat. The stimuli used were passive distension (urinary bladder, colon), isovolumetric contraction (urinary bladder), movements of the urethral catheter and mechanical shearing stimuli (mucosal skin of the anal canal). (1) In total 245 afferent units which projected in the pelvic nerve were isolated from the sacral dorsal roots. From one of the following organs, urinary bladder, colon, urethra and anus 117 afferent units were activated. By these stimuli from the bladder, urethra and anus 122 afferent units could not be activated, and as far as tested also not from the colon; in 6 afferent units the classification was unclear. (2) Afferent units from the urinary bladder and the colon responded consistently to passive distension of the respective organ. The units from the urinary bladder showed graded responses at intraluminal pressures of about 10–70 mmHg and responded also to isovolumetric contractions of the organ. The thresholds of the units from the bladder to passive distension and contraction varied from about 5 to 20 mmHg intravesical pressure. (3) The afferent units from the urethra and the anus did not react or showed some weak phasic and irregular responses to distension and contraction applied to the urinary bladder or to distension of the colon. They were consistently excited by low threshold mechanical stimulation of the urethra and anus, respectively. (4) The axons from the bladder, urethra and anus were presumably myelinated (conduction velocity above 2 m/s) and conducted at 10.3 ± 6.1 m/s ($n = 34$, mean ± SD), 26.3 ± 9.3 m/s ($n = 13$) and 9.5 ± 5.1 m/s ($n = 37$), respectively. The axons from the colon conducted at about 0.5 to 16 m/s ($n = 20$), 13 of them conducting at less than 2 m/s. About 75% of the axons which could not be activated by mechanical stimulation of the visceral organs were presumably unmyelinated (conduction velocity below 2 m/s). (5) Some ongoing activity was found in 9 out of 26 afferent units from the anus but, with one exception, the afferent units from the bladder, urethra and colon were silent. (6) It is concluded that the pelvic afferent units from the urinary bladder, urethra, colon and anus consist of distinct populations with characteristic response patterns. There is no indication from this investigation that the urinary bladder is supplied by sacral afferents which are only recruited at high intravesical pressures during passive distension and isovolumetric contractions and which are possibly associated with pain.

Key words: Sacral visceral afferents – Pelvic nerve – Urinary bladder – Urethra – Colon – Anus – Functional properties – Cat

Introduction

The distal urinary tract, distal colon, rectum and anus are supplied by lumbar and sacral visceral afferent neurones. The lumbar primary afferent fibres pass through the lumbar splanchnic, hypogastric and lumbar colonic nerves and have their cell bodies in the dorsal root ganglia L3 to L5 [2, 8, 9, 39]. The sacral afferents pass through the pelvic nerves and have their cell bodies in the sacral dorsal root ganglia S1 to S3 [38]. In addition the urethra and probably also the distal skin of the anal canal are innervated by somatic afferents which pass through the pudendal nerve [48].

Lumbar afferents from hindgut and lower urinary tract are excited by mechanical and chemical stimuli [6, 11, 23, 27, 40, 41]. Excitation of these afferents may elicit painful and non-painful sensations from the urinary bladder [26, 28, 46] and from the colon. The functional role of these afferents in organ regulation is not clear (but see [25]). Excitation of the sacral afferents by adequate stimulation may also elicit various painful and non-painful sensations from the organs. For the urinary bladder these sensations include sensation of fullness, desire to micturate, sensation of impending micturition and pain when the organ is distended [17, 44] and possibly even touch and temperature sensations upon stimulation of the mucosa ([26, 36, 37, 45]; but see also refs. [12, 43, 44]). The sacral visceral afferent supply of the lower urinary tract and the hindgut is essential for the neuronal regulation of evacuation (micturition and defaecation) and continence of the organs [16, 47]. Furthermore, stimulation of these afferents elicits very specific reflexes in lumbar sympathetic neurones supplying pelvic organs and colon [7, 10, 32] and skeletal muscle and skin [31].

Very little is known about the functional properties of these afferents. Sacral visceral afferents from the urinary bladder that pass through the dorsal roots are supposed to react to contraction and passive distension of the organ at intravesical pressures which occur during normal micturition as well as at pressures which are accompanied by pain [22, 29, 30, 42, 51]. It is not clear whether there exist sacral

* Supported by the Deutsche Forschungsgemeinschaft

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visceral afferent neurones which respond only to contraction and distension stimuli of the urinary bladder at high intravesical pressures that are associated with pain. Sacral visceral afferents which project through the ventral roots respond to distension and contraction of the urinary bladder, to distension of the colon and of the urethra and to mechanical, thermal and chemical stimulation of the intestinal mucosa [13, 15, 24].

The present paper concentrates on the neurophysiological analysis of sacral visceral afferents from the lower urinary tract and the hindgut (distal colon, rectum and anus) which project to the spinal cord through the dorsal roots. The stimuli used in order to excite the afferents were distension, contraction, shearing stimuli and other mechanical stimuli. Preliminary results have been published in previous communications [4, 5, 33].

Methods

The experiments were performed on 19 male cats and one female cat (weight 2.0–6.1 kg). The cats were initially given 10–15 mg/kg ketamine hydrochloride (Ketanest, Parke-Davis, Ann Arbor, MI, USA) i.m.; α-chloralose (45–60 mg/kg, solution of 1% in saline) was subsequently administered i.v. through the jugular vein. Additional chloralose was given in doses of 30–50 mg i.v. if required. The criterion for establishing a sufficient depth of anaesthesia was the persistence of miotic pupils. In total about 80–120 mg/kg α-chloralose was given throughout an experiment. All animals were artificially ventilated via a tracheal canula and immobilized by i.v. injections of pancuronium bromide (Pancuronium, Organon, Oss, The Netherlands; about 0.6 mg/h). The arterial blood pressure was recorded continuously from the right common carotid artery. The end-expiratory CO_2 was adjusted to 3–4 vol%. The body core temperature was recorded intraesophageally and kept close to 38° C by an automatically regulated heating plate.

The left pelvic nerve was exposed through the upper sciatic notch between the sacral bone and the hip bone. For this purpose the dorsal rim of the hip bone was removed. The pelvic nerve was separated from the medial haemorrhoidal artery and the rectal wall for a distance of about 6–8 mm by a piece of plastic film and put on a pair of flexible platinum electrodes for electrical stimulation. The sciatic nerve, the pudendal nerve and as many muscle branches as possible of the sacral spinal nerves were cut on the left side; furthermore, the tail was amputated about 2 cm distal to its origin. These latter procedures abolished a large part of the afferent input through the sacral spinal nerves from skeletal muscle and skin.

Thin bundles with single or few afferent fibres were isolated either from the dorsal root S2 (18 experiments) or S1 (2 experiments). The afferent activity was recorded monopolarly with a fine platinum wire electrode against a platinum reference electrode positioned nearby. Most afferent units (233 out of 245 units, 95%) were identified by their responses to electrical stimulation of the pelvic nerve with single impulses (see inset record in Fig. 9). The other afferent units were identified by way of the invariant shape of their extracellularly recorded action potentials. The distance between the stimulating electrode in the pelvic nerve and the recording site was 45.3 ± 12.8 mm (mean ± SD, $n = 17$). In all experiments a catheter was introduced through the urethra into the urinary bladder to fill the bladder with fluid and to measure intravesical pressure [6]. In 7 experiments a thin-walled rubber balloon was inserted into the distal colon. The balloon had a length of 5–7 cm and was positioned from about 3–10 cm proximal to the anus. The balloon was mounted at the end of a flexible tube through which it was filled with saline and the pressure was measured by way of a pressure transducer.

The following mechanical stimuli were used in order to excite the afferent units: (1) The urinary bladder was passively distended either to preset intravesical pressures of 10–100 mm Hg as described by Bahns et al. [6] or by injecting successively volumes of 5–10 ml saline through the urethral catheter. (2) After slow injection of 10–30 ml fluid into the urinary bladder through the urethral catheter the urinary bladder contracted isometrically in only 9 of the 19 experiments. Contractions in the other experiments were induced by electrical stimulation of the pelvic nerve, in order to determine the threshold pressure at which the afferent units were activated. We have no explanation why the urinary bladder did not contract actively in 10 of our experiments. (3) The distal colon was distended by injecting water into the intracolonic balloon. (4) Afferent units from the urethra were stimulated by small movements of the urethral catheter (tapping, pulling and lateral movements, see [6]). (5) Afferent units from the mucosa of the anus were stimulated by mechanical shearing and pressure stimuli applied by a spatula.

The data were recorded simultaneously "on-line" by a MINC RT 11 computer and analyzed "off-line" by a PDP 11/60 computer. Additionally the recordings were taken on magnetic tape and photos from the original records were taken from a storage oscilloscope by a Nihon Kohden 3A camera.

Results

The results were obtained from 245 single afferent units and 10 multiunit bundles. A total of 117 single units (48%) could be excited by mechanical stimuli from one of the following organs: urinary bladder, urethra, anal canal and colon, whereas 122 units (49%) could not be excited from these organs and for 6 units the activation by mechanical stimuli was unclear.

Afferent units excited from the urinary bladder

By distension and (as far as tested) by isovolumetric contraction of the urinary bladder 43 afferent units were excited. Out of these 5 units were also activated by movements of the urethral catheter. Mechanical stimulation of the mucosal skin of the anus and distension of the colon did not excite the afferent units. The afferent units had no ongoing activity when the bladder was empty (30 units tested).

Passive distension of the urinary bladder elicited either static responses or, particularly at high intravesical pressures, dynamic responses followed by static responses (Fig. 1). The activity increased with increasing intravesical pressures (Fig. 1). At the end of the pressure steps the activity decreased rapidly; only occasionally were afterdischarges observed.

Fourteen afferent units were investigated systematically for their stimulus-response relations to passive distension at intravesical pressures of up to 100 mm Hg. The activity in all units increased with increasing intravesical pressures; for

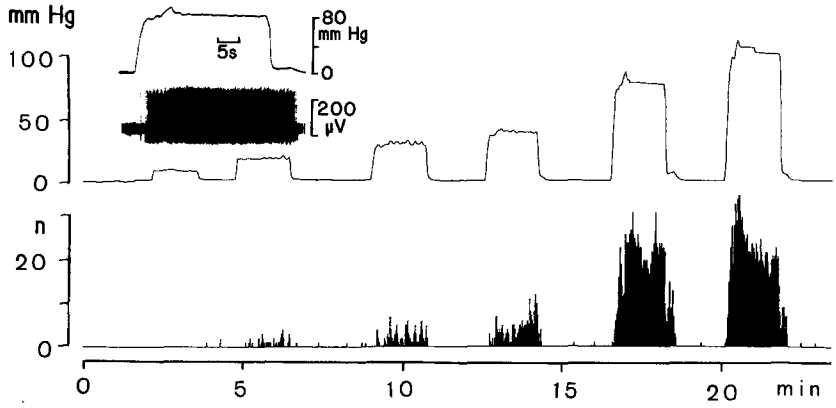

Fig. 1
Responses of an afferent unit to passive distension of the urinary bladder to preset intravesical pressures. The urinary bladder produced small contractions during the distension. The inset record illustrates the response to a pressure step of about 80 mm Hg. *Ordinate scale* in *lower histogram* imp/2 s

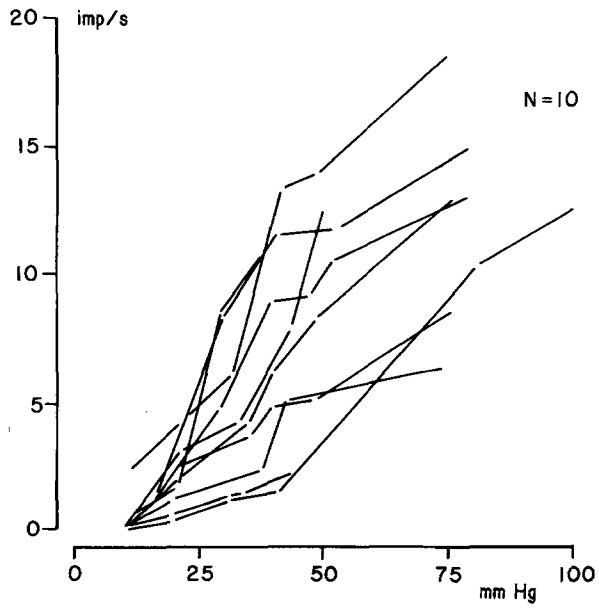

Fig. 2. Stimulus-response relations of the activity in sacral afferent units from the urinary bladder to passive distension of the bladder. *Ordinate scale:* mean impulse rate during periods of distension of 50–90 s

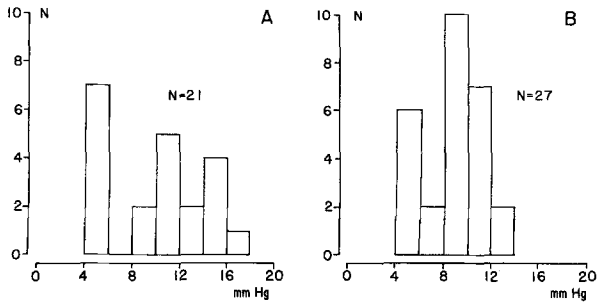

Fig. 3. Distributions of the response thresholds of afferent units to passive distension (**A**) and to isovolumetric contraction (**B**) of the urinary bladder. The threshold values to distension were either extrapolated from the stimulus-response curves (see Fig. 2) or taken from the responses to small individual distensions. The threshold values to the contractions were taken from the responses to small individual contractions which either occurred spontaneously or were evoked by electrical stimulation of the pelvic nerve. The smallest contraction pressure which produced an excitation of an afferent unit with 2–3 spikes or the intravesical pressure at which an afferent unit was first excited was taken as threshold (see [6])

10 of them the stimulus-response relations are shown in Fig. 2. In some experiments small pressure fluctuations were observed during the distension stimuli (see Fig. 1), indicating that the urinary bladder contracted when it was "isotonically" distended. These contractions might have contributed quantitatively to the excitation of the visceral afferents elicited by the distensions. We analyzed therefore the responses to distension in 4 afferent units before and after spinalization at L6/L7. The intention was to abolish the contractions of the urinary bladder. Surprisingly, the contractions were reduced in size and frequency but not totally abolished. The stimulus-response curves for the excitation of the afferent units were indistinguishable before and after spinalization. The response properties of the sacral visceral afferents to distension and slow filling of the urinary bladder are now tested in our laboratory before and after cutting the sacral ventral roots.

The threshold pressures for exciting the afferent units were determined either from the stimulus-response curves or from the minimal pressures which led to an excitation of them. It was found that all afferents reacted to distension of the urinary bladder at intravesical pressures of less than 20 mm Hg (Fig. 3A; mean ± SD: 9.5 ± 3.8 mm Hg, $n = 21$). Some afferent units were weakly activated only at intravesical pressures of 30 mm Hg or more to passive distension of the urinary bladder, these units exhibited responses to light movements of the urethral catheter (see below).

All afferent units which were activated by passive distension were also excited during active contraction of the organ. The temporal shape of the intravesical pressure was well encoded by the discharge rates of the afferent units. This is seen in the multi-unit as well in the single unit activity (Fig. 4). The intravesical threshold pressures for activating the afferent units were determined from the responses to small isovolumetric contractions which occurred either spontaneously or which were evoked by electrical stimulation of the pelvic nerve. These threshold pressures varied between about 5 and 15 mm Hg (Fig. 3B; mean ± SD: 8.2 ± 2 mm Hg, $n = 27$).

Afferent units excited from the urethra

By tapping on or light movements of the urethral catheter 14 afferent units were excited. Figure 5B, C illustrates the reactions of a typical unit to single or frequent lateral movements of the catheter. The afferent unit responded vigorously to this stimulus.

These afferent units were not activated by stimulation of the anal skin (9 units tested) and by distension stimuli applied to the colon (6 units tested). Distension of the urinary bladder activated 5 out of 11 afferent units. This activation consisted of short burst-like responses which occurred either at the beginning or at the beginning and the end of distension stimuli of 30 mm Hg or more. During the distension there was either no response or, at high intravesical pressures, a low frequency discharge of less than 1 Hz (Fig. 5A).

With one exception, the afferent units which were activated from the urethra exhibited no ongoing activity. One unit discharged spontaneously with 0.9 imp/s.

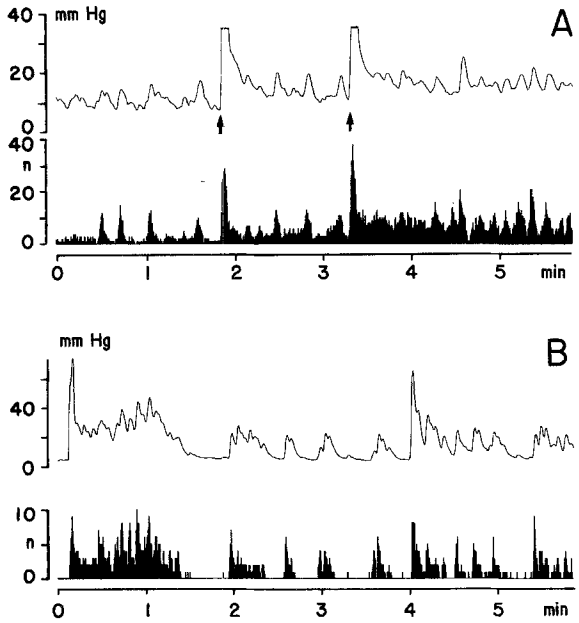

Fig. 4A, B. Responses of sacral afferent units to isovolumetric contractions of the urinary bladder. **A** Activity in a multiunit filament. At the beginning of the record the volume in the urinary bladder was 45 ml; at each of the times indicated by the *arrows* 5 ml saline were injected in the bladder through the urethral catheter. **B** Single unit activity. *Ordinate scales* of *lower histograms* impulses/0.5 s

Afferent units excited from the mucosal skin of the anus

By mechanical stimulation of the mucosal skin of the anal canal 40 afferent units were excited. Most effective were shearing stimuli (movements) applied with a spatula in cranio-caudal direction. Static tactile, distension and circular shearing stimuli were less effective (Fig. 6A, B). Stimulation of the urethra, as described above, did not activate the units (22 units tested). Out of 36 units 5 were activated by distension of the urinary bladder. However, these discharges occurred very irregularly and either only at the beginning of the distension or some 10–30 s after the beginning of the distension. Figure 6C illustrates one example. The frequency of the discharges during or after distension of the urinary bladder was one per second or less. Eight afferent units which were activated from the anal skin were tested for their responses to distension of the colon. Only one afferent unit was weakly activated.

Most afferent units which were activated from the anal skin were silent (19 out of 27 units tested). Eight units displayed some ongoing activity, two of them discharged with 0.5 and 0.2 Hz, respectively, and the other six units at rates of less than 0.1 Hz.

Afferent units excited from the colon

In 7 experiments 20 afferent units were found which were activated by distension of the colon. Figure 7 illustrates a typical experiment: distension of the colon led to a continuous activation of the afferent unit which increased with increasing intraluminal pressure. Release of the volume from the balloon in the colon stopped the discharge of the afferent unit (Fig. 7D). Some of the afferent units displayed only phasic responses during passive distension of the colon in the first 10–20 s. Activity in 3 multiunit bundles which contained only unmyelinated fibres upon stimulation of the pelvic nerve (see below) exhibited the same behaviour to distension of the colon as the single units. No systematic attempt was made to analyze the responses of the units to colon distension quantitatively. The intraluminal threshold pressures at which these units were activated were in the range of 15–40 mm Hg.

The afferent units which were activated from the colon were not activated from the urinary bladder (distension); one unit was weakly activated from the urethra (tapping on

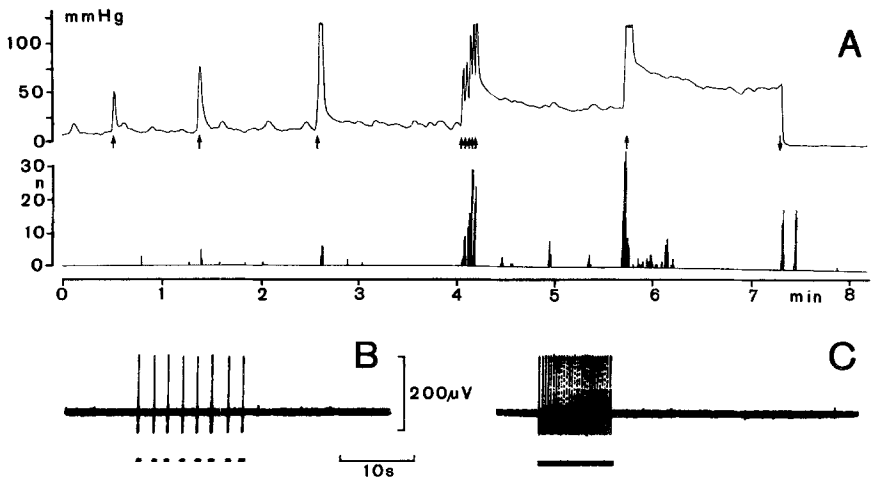

Fig. 5A–C
Responses of a single afferent unit from the urethra to distension of the urinary bladder and to movements of the urethral catheter. **A** Distension of the urinary bladder. At the beginning of the record the bladder contained already 40 ml saline. At the 1st, 2nd, 3rd and 9th *arrow* an additional 5 ml saline each was injected in the bladder. At the 4th to 8th *arrow* 10 ml saline was injected in five fast steps. At the 10th (inverted) *arrow* the volume was released from the bladder. Note the phasic excitations of the afferent unit during the injections and with emptying of the bladder. Ordinate scale in lower histogram impulses/0.5 s. **B** Single lateral movements of the urethral catheter. **C** Fast lateral movements of the catheter

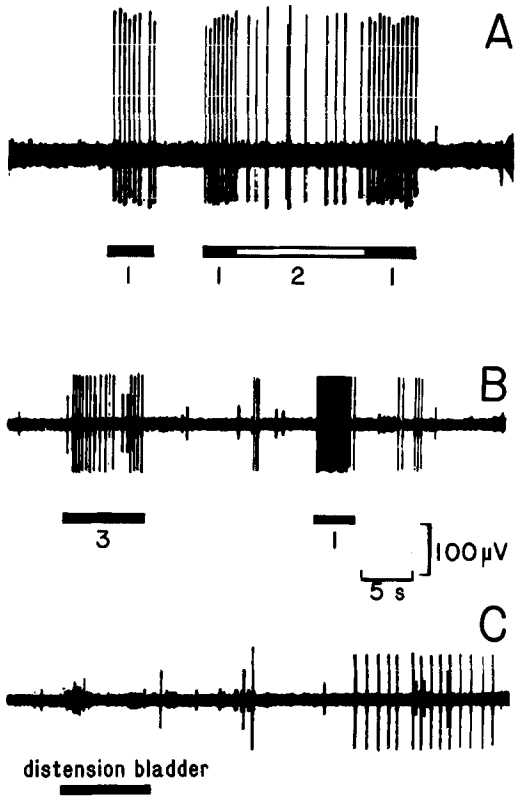

Fig. 6. Responses of two single afferent units (**A** and **B, C**) from the mucosal skin of the anus to mechanical stimuli. **A, B** Local mechanical stimuli. Rostro-caudal shearing stimuli are most effective (stim *1*); other stimuli (circular shearing, stim *2*; distension, stim *3*) are less effective. **C** Distension of the urinary bladder by a bolus injection of 10 ml saline. Note that the afferent unit discharged about 20 s after the injection

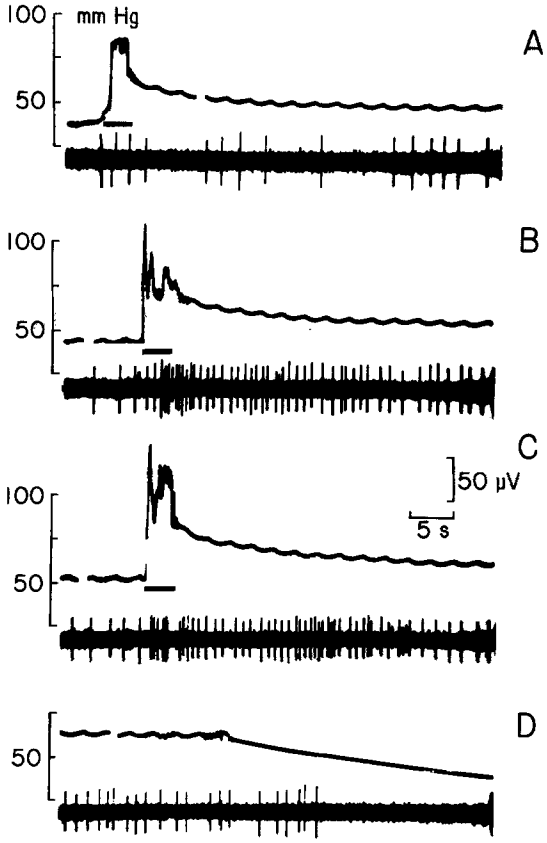

Fig. 7A–D. Reaction of a single afferent unit to distension of the colon. At the beginning of the record in **A** the balloon in the colon contained 50 ml water. In **A, B** and **C** each 5 ml water was slowly injected in the balloon (*black bars*). In **D** the balloon was emptied

and movement of the urethral catheter), and one unit was weakly activated by mechanical shearing stimuli applied to the anal canal. The afferent units from the colon displayed no ongoing activity when the colon was empty.

Conduction velocities of visceral afferent axons projecting in the pelvic nerve

The conduction velocities were measured on the distance between the stimulation electrode at the pelvic nerve and the recording site at the dorsal roots. The latencies were determined at stimulus strengths which were about 2 times the threshold for exciting the axons which conducted at more than 2 m/s and about 1.5 times the threshold strength for exciting the axons which conducted at less than 2 m/s. The inset in Fig. 9 shows the record of the signals from eight afferent units which were elicited by electrical stimulation of the pelvic nerve with single pulses. One unit (indicated by a star) conducted at 10 m/s. This unit was activated by distension and contraction of the urinary bladder. The other units (indicated by dots) conducted at 1.5 – 0.5 m/s and were not activated by any of the natural stimuli used. The axons of these units were presumably unmyelinated.

Figure 8 illustrates the distributions of the conduction velocities of the afferent axons which were functionally identified. Visceral afferents which could be activated from the urinary bladder conducted at 10.3 ± 6.1 m/s ($n = 34$;

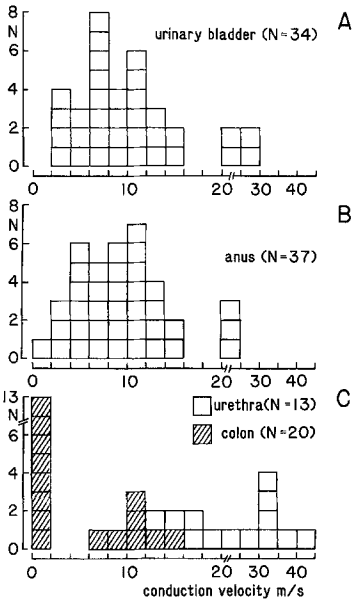

Fig. 8A–C. Distributions of the conduction velocities of the axons of the functionally identified sacral afferent units. The conduction velocities were determined between the stimulation electrode at the pelvic nerve and the recording site. **A** Afferent units activated from the urinary bladder. **B** Afferent units activated from the anus. **C** Afferent units activated from the urethra and colon

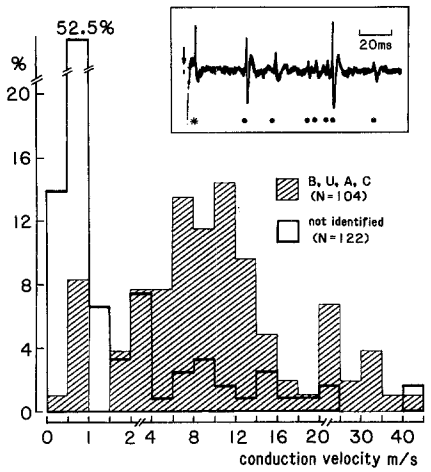

Fig. 9. Distributions of the conduction velocities of the axons of the functionally identified afferent units (*shaded histogram;* B, bladder; U, urethra; A, anus; C, colon) and of afferent units which could not be activated from the bladder, urethra, and anus (*solid line histogram*). Out of the latter units 89 were tested for their responses to distension of the colon and did not react; 33 units were not tested upon their reaction to colon distension. The *inset* shows a record from a bundle with 8 afferent axons which were activated by electrical stimulation of the pelvic nerve with single pulses (*arrow*; 14 V, 0.5 ms pulse duration). The unit marked by a star was activated by contraction and distension of the urinary bladder. The units marked by dots conducted at less than 1.5 m/s and were not activated by any of the mechanical stimuli used

mean $\pm$ SD), from the urethra at 26.3 $\pm$ 9.3 m/s ($n = 13$) and from the anus at 9.5 $\pm$ 5.1 m/s ($n = 37$). Only one of these units conducted at a speed which was below 2 m/s; i.e. practically all afferents were presumably myelinated. Afferent axons which were activated from the colon conducted at about 0.5–16 m/s (Fig. 8C). Out of 20 afferents 13 were presumably unmyelinated (conduction velocity below 2 m/s).

A total of 122 axons which projected through the pelvic nerve could not be activated from the urinary bladder, urethra and anus. Out of these afferents, 89 were also tested for their responses to distension of the colon and were not activated from this organ, and 33 of these afferents were not tested for their responses to colon distension; a few of them were to be activated from the colon. Figure 9 illustrates the distribution of the conduction velocities of the afferent axons which could not be excited by stimulation of the pelvic visceral organs (solid line histogram) in comparison to the distribution of the conduction velocities of the functionally identified axons (shaded histogram). About 76% of the visceral afferent axons which were not functionally identified conducted at less than 2 m/s and were presumably unmyelinated, whereas only 14% of the functionally identified axons conducted at less than 2 m/s and practically all of them were activated from the colon.

Discussion

In the present paper the responses to mechanical stimulation of spinal pelvic visceral afferent neurones which project through the sacral dorsal roots are described. For their classification and characterization only mechanical stimuli, such as distension (urinary bladder, colon), isovolumetric contraction (urinary bladder), shearing and pressure stimuli (anus) and movements of the urethral catheter, were used. Four different types of afferent units were discriminated with respect to the urinary bladder, urethra, anal skin and colon. Most units responded to the stimulation of one organ only. A few units were excited to stimulation of two organs; these units reacted, however, reproducibly to stimulation of one organ but weakly and irregularly to stimulation of the other one. The organs were left in situ, the peritoneal cavity was not opened and the receptive fields of the afferent units were not determined. The reproducibility of the responses to the stimuli used argues strongly that the afferent units were anatomically associated with the respective organs. The excitation of the afferents by the stimuli used leads to distinct reflexes in parasympathetic neurones which supply the lower urinary tract and the hindgut [16, 47] and in lumbar sympathetic neurones [7, 10, 31, 32]. Additionally the excitation of these populations of afferent neurones by mechanical stimulation leads to various types of sensation from these organs including pain ([20, 21, 44], see [33, 47]).

The afferent units from the urinary bladder are silent and respond in a graded manner to passive distension and contraction of the urinary bladder. The response characteristics of these afferent units are similar to those reported in the literature [22, 29, 30, 51]. Our results are at variance with those of Arlhac [3] who reported that his slowly adapting units from the urinary bladder which were excited by passive distension and contraction have resting activity and that some of his slowly adapting units responded to contraction of the organ only but not to distension. Pelvic afferent units which are reported in the literature as being very sensitive to phasic stimuli, such as vibration stimuli, [3, 22, 51] are probably identical with our units which were excited from the urethra. No data are available in the literature about afferents from the anal mucosal skin and only Floyd and Lawrenson [22] reported slowly adapting pelvic afferents which respond to distension of the colon.

Most of the sacral afferents which are activated by distension of the colon are unmyelinated (see Fig. 8C). This is consistent with the finding of de Groat and coworkers [17, 18] who showed that the afferent limb of the spinal defaecation reflex pathway is unmyelinated. The same authors claim that the afferent limb of the micturition reflex pathway through the upper pons in adult cats is myelinated and through the sacral spinal cord in chronic spinal cats unmyelinated [16, 18, 19]. In our investigation on intact cats only myelinated pelvic afferent fibres (conduction velocity above 2 m/s) were activated by distension and contraction of the urinary bladder (see Fig. 8A).

Some interesting differences exist with the results obtained on visceral afferent units which project in the sacral ventral roots [13, 15]. The ventral root afferents have their cell bodies in the dorsal root ganglia and most of them are unmyelinated [1]. The conduction velocities of these afferent axons were determined between two closely positioned pairs of recording electrodes at the ventral root filaments [13]. These axons may be collateral branches of visceral afferent neurones which project through the dorsal roots to the spinal cord (see [35]) or may loop through the ventral roots before they enter the spinal cord through the dorsal roots or may have no dorsal root process (see [14]).

Most unmyelinated ventral root afferents which were activated from the urinary bladder were reported to respond to passive distension but not to contraction of the organ, a few of these axons had a low rate of ongoing activity.

Myelinated afferent axons from the urinary bladder responded to both contraction and distension [13, 15]. Ventral root afferents from the urethra were unmyelinated and responded to distension of the organ [13]. Ventral root afferents from the mucosa of the anus were unmyelinated and had high mechanical thresholds, some of them responding to cold, warm and chemical stimuli; no afferent units with low thresholds were found [13]. Only ventral root afferents from the colon and rectum which responded to distension of the organ were similar in their functional properties to our afferents from the colon. Other ventral root afferents from the colon-rectum were activated by stimulation of the mucosa.

The comparison of the functional properties of the sacral visceral afferents in the ventral roots [13, 15] with the functional properties of the sacral visceral afferents in the dorsal roots leads to the following conclusions: (1) Many unmyelinated ventral root afferents from the urinary bladder, urethra and intestinal mucosa cannot be branches of visceral afferent neurones which project in the dorsal roots and which have functional properties as described in the present paper. (2) Sacral ventral root afferents which are activated from the mucosa of the hindgut and the urethra could be collaterals of the visceral afferent neurones which are not activated by the mechanical stimuli used in the present investigation (see Fig. 9). We did not test our neurones for their responses to damaging mechanical and other stimuli applied to the mucosa. (3) Myelinated sacral ventral root afferents which are activated by passive distension and contraction of the urinary bladder and ventral root afferents which are activated by colon distension could be collaterals of afferent neurones which project in the dorsal roots. Preliminary experiments conducted in our laboratory illustrate that very few afferents in the ventral root S2 can be activated by electrical stimulation of the dorsal root S2 [34]. Finally, several afferent units from the urethra and anus which are reported by Clifton et al. [13] may have travelled through the pudendal nerve.

The afferent units from the urinary bladder reacted in a graded manner to passive distension of the organ and encoded in their discharge rate the intravesical pressure. The intravesical threshold pressures for exciting all afferent units were in the range of 5–20 mm Hg. These values are the same as those reported by Floyd and Lawrenson ([22], reported in [42]) but somewhat lower than the threshold pressures for exciting the lumbar visceral afferents from the urinary bladder (t-test, $p < 0.05$; [6]). We did not find sacral unmyelinated afferent units which were activated by mechanical stimuli (passive distension, contraction) from the urinary bladder. The intravesical threshold pressures for exciting unmyelinated ventral root afferents by passive distension of the urinary bladder are probably in the range of about 15–25 mm Hg (seven values estimated from the figures in [13, 14]) and somewhat higher than those of the dorsal root afferents (see Fig. 3 A). Clinical experiences in humans argue that pain from the urinary bladder is due to excitation of lumbar as well as sacral visceral afferents [49, 50]. Investigations conducted recently on the lumbar afferent supply of the lower urinary tract [6] and the present investigation of the sacral afferent supply of the lower urinary tract (see also [42]) failed to show that visceral afferent neurones exist which can only be activated at intravesical pressures of more than 30–40 mm Hg; all distension sensitive lumbar and sacral afferent neurones from the urinary bladder which project through the dorsal roots to the spinal cord seem to be activated at intravesical pressures which occur during normal micturitions. These results could imply that the sacral afferent units from the urinary bladder which are involved in nociception and pain, elicited by high intravesical pressures, pass through the sacral ventral roots and/or that pain occurring during high intravesical pressures is triggered by the activity in the same afferents which are also excited during normal micturition (see [33]). Further experiments are needed to study the discharge of afferents from the urinary bladder to stimuli other than distension (e.g. mechanical, chemical and thermal stimuli applied to the mucosa) and to inflammatory conditions which occur in humans and which may be accompanied by pain.

Acknowledgement. We acknowledge gratefully that Joachim Häbler, Martin Koltzenburg and Nicole Lobenberg conducted fully independently some of the experiments as described in this paper. The data obtained in these experiments were integrated in this paper and served as valuable control for our measurements.

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Received September 8, 1986/Received after revision May 14/Accepted May 30, 1987