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Interspike Intervals of Secondary Muscle Spindle and Urinary Bladder Afferents in Relation to the Oscillation Periods of Sacral Spinal Oscillators for Continence in Man

G. SCHALOW, U. BERSCH, K. GÖCKING, G.A. ZÄCH

Schweizer Paraplegiker-Zentrum, Nottwil, Switzerland

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Summary

Two pairs of wire electrodes were used to record afferent and efferent single fibre extracellular action potentials (APs) from human nerve root filaments. The nerve fibres were identified according to the group to which they belong by comparing the afferent and efferent conduction velocity distribution histograms and identifying peaks and ranges of nerve fibre groups. Secondary muscle spindle afferents and α_2-motoneurones (FR) were identified by having the same peak group conduction velocity (calibration relation), which is 50 m/s at 36 °C. On the basis of AP wave form comparisons, the natural impulse patterns of five secondary muscle spindle afferents, two fusimotor motoneurones and two oscillatory firing α_2-motoneurones could be identified in the dorsal S4 root. The patterns of single endings of secondary spindle afferent fibres could be identified. The shortest interspike intervals of single endings of all secondary muscle spindle afferents had the same duration as the shortest interspike intervals of the two fusimotor fibres (80 ms) and equalled a half of the oscillation period of one repetitively firing α_2-motoneurone (6 Hz) probably innervating the external anal sphincter (three AP impulse train firing). In another more rostral dorsal root filament (probably S3 or S2) of the same human, the interspike intervals of six secondary spindle afferents were more variable. The values of peaks in the interspike interval distributions ranged from 60 to 102 ms. In the coccygeal root, the interspike interval duration ranged from 160 to 185 ms, directly contributing to the drive of the oscillatory firing α_2-motoneurone. The different agreement between the oscillation period and the interspike intervals of the spindle afferents in different segments indicate that the oscillatory firing CNS circuitry was localized within S3 to S5 segments of the conus medullaris for the drive of the anal sphincter. An α_2-motoneurone firing repeatedly with 1 to 2 AP impulse trains, innervating most likely the external urethral sphincter, fired at a frequency of 9.1 to 6.7 Hz, a similar frequency of the oscillation as the interspike intervals from two activated stretch receptors of the urinary bladder wall. The measurements of this brain-dead human indicates that in this case the neuroneal circuitry driving the external anal sphincter was mainly confined to the sacral micturition and defecation centre, mainly located in the S3 to S5 segments.

Key Words

Secondary spindle afferents – Rhythm generator – Single fibre action potentials – Oscillation period – Urinary bladder afferents – Continence – Man

Introduction

The aim of this research was to reconstruct continence functions of the urinary bladder and rectum in man with spinal cord lesions (paraplegics). Anastomosis could be a possible treatment of this state (Schalow *et al.* 1992, Schalow and Barth 1992b, Schalow 1992b,c). Branches of intercostal nerves from supralesional levels have to be "connected" to cauda equina nerve roots to reinnervate the bladder. Following spinal cord lesions a detrusor-sphincteric dyssynergia often occurs. Among other reasons, such a disorder can be due to the disconnection from the pontine micturition centre (Holstege 1992, Kruse *et al.* 1991) or to interneuronal cell death of the sacral micturition centre following spinal cord asphyxation

with a loss of plasticity (Gelfan and Tarlov 1959, van Harreveld 1962, 1964, Krogh 1945, 1950). Therefore, before reconnecting nerves to renew bladder functions, the physiological and pathophysiological functions of the involved spinal cord circuitry have to be understood better to see whether such treatment could be successful.

To be able to analyse human nervous system functions, a classification scheme for the human peripheral nervous system has been developed in which nerve fibre groups are characterized by group conduction velocities and group nerve fibre diameters (Schalow 1991a, Schalow and Barth 1992a). The classification schemes of Grundfest, Erlanger and Gasser (Gasser *et al.* 1939) and Lloyd and Hunt (Lloyd 1943), in which nerve fibre classes are characterized by ranges of conduction velocities (and diameters) designated as A, B and C or I, II, III and IV, firstly do not apply to man and secondly they are too inaccurate. With this new human classification scheme, in combination with the method of recording single fibre action potentials (APs) with two pairs of wire electrodes, it is possible to record natural impulse patterns from afferent and efferent nerve fibres in the same root filament simultaneously. With AP wave form analyses it is possible to split the summed AP activity of, for example, a sacral dorsal nerve root at least partly into impulse patterns of single dorsal root afferent and dorsal root efferent fibres (Schalow 1992d). It is therefore possible to analyse the function of different populations of receptors (Schalow 1992c), natural motoneuroneal responses, to correlate afferent and efferent impulse patterns of single fibres, and to study in this way the functions of circuitries of the human CNS under physiological and pathophysiological conditions (Schalow 1991b, 1993a). At present there is no other comparable effective electrophysiological method available, for studying such details of natural functions of the human peripheral and central nervous system (CNS).

Especially the human urogenital system can be studied in detail because of the unique anatomical situation in the caudal spinal canal. Because of the ascensus of the medulla and because humans have no tail, the lower sacral roots are thin, long and the innervation of the urogenital system is not mixed with functions to the tail as in the rat, cat or dog. The mixing of afferents and efferents in the lower sacral ventral (Schalow 1989) and dorsal roots (Schalow 1991a, 1992d) allows the recording of single afferent and efferent fibres without dissecting and damaging them, since afferent and efferent extracellular APs can be distinguished from each other by an opposite triphasic AP wave form and an reciprocal conduction time. Because of this anatomical situation and the possibility of measuring CNS circuitry alterations precisely with oscillatory functional changes, the functions of the human urogenital system can be studied in detail, which makes it likely that physiological treatment can be found in the future for urinary bladder dysfunction (Kruse *et al.* 1991, Torrens and Morrison 1987).

In this paper, the firing patterns of secondary spindle afferents are mainly under consideration. These drive spinal circuitries and innervate muscle spindles of the external anal sphincter and pelvic floor muscles contributing to continence. The external bladder sphincter probably contains no muscle spindles. Interspike intervals of muscle spindle afferents have so far been measured in man only outside the urogenital range (Vallbo 1974, Vallbo *et al.* 1979, Burke *et al.* 1979). These data are probably only partly comparable with those obtained here, especially since it seems that some muscle spindles in the sacral range are also innervated by parasympathetic efferents (Schalow 1993d). Evidence for autonomic muscle spindle innervation has been found in animals histologically (Barker and Saito 1981) and functionally in response to sympathetic stimulation (Passatore *et al.* 1985). Gamma-reflex activity in cats is still being studied (Dickson *et al.* 1993).

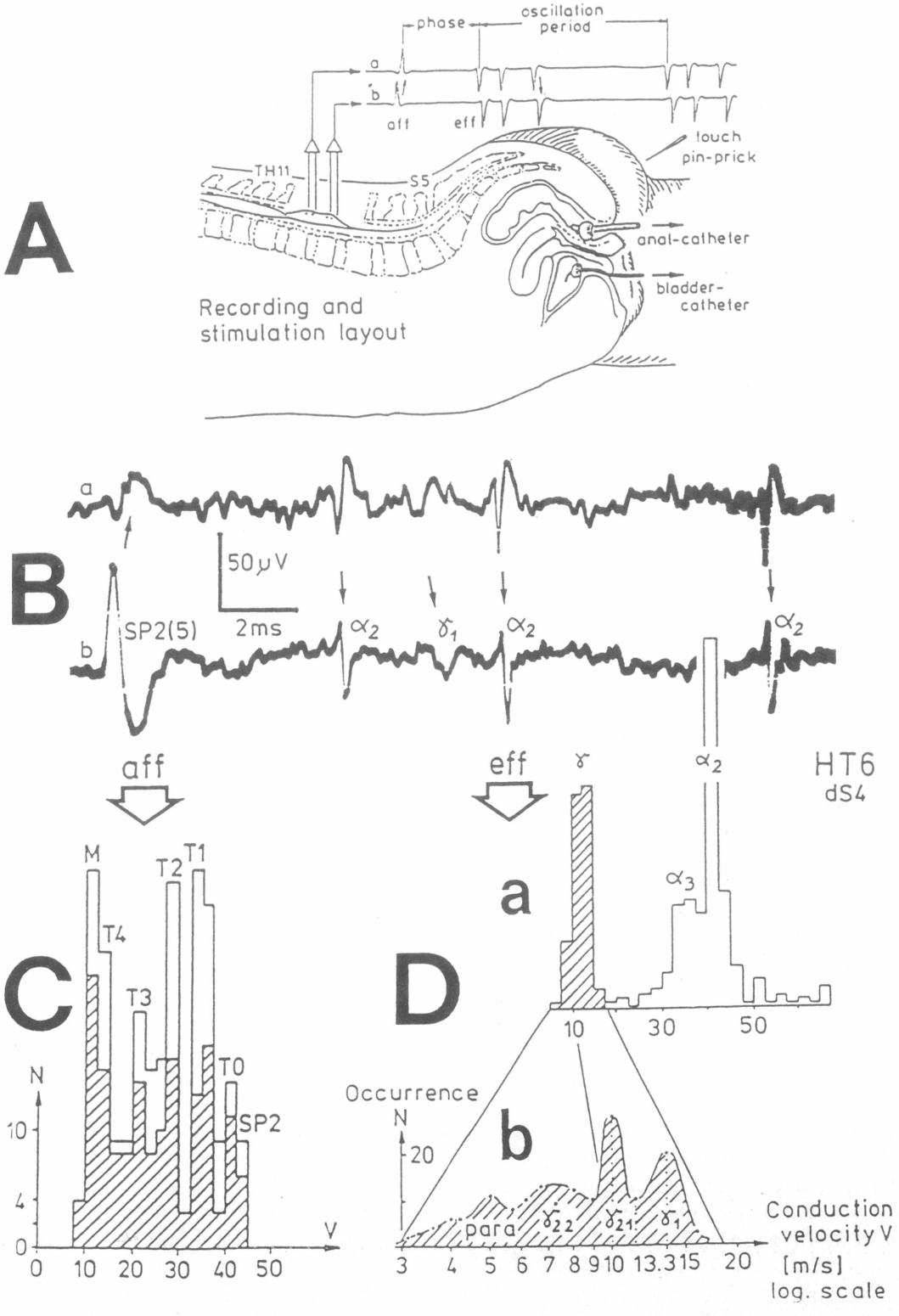
This paper is a continuation of studies concerning human nervous system functions (Schalow 1993a,b,c,d).

Materials and Methods

The methods were partly described in previous publications (Schalow 1991a, Schalow and Barth 1992a). The data were obtained from one brain-dead human. The blood pressure in the brain-dead human was maintained by the administration of dopamine (4 g/kg per min), as in kidney removals.

The measurements were done in accordance with the Helsinki Declaration and were performed to reconstruct urinary bladder function as in kidney removals. The measurements (performed in 1988) were approved by the Ethical Committee of the GDR. As soon as the Committee decided that the patient was brain-dead, the patient was considered as a cadaver and no longer as a patient. Mostly, the cadavers were transferred to the urology department for kidney explantation or, after switching off the respirator, the cadaver was transferred to the pathology department for autopsy. The measurements on the brain dead human cadaver were performed before autopsy. The opening of the body for the measurements is a minor one in comparison to those at autopsy. If close relatives were against obduction, the measurement would have not been performed. Previous animal experiments were necessary for basic clinical research. However, certain information cannot be obtained from animals, and more relevant knowledge can be obtained from human cadavers. The measurements should serve to improve the function of the sacral ventral root stimulator for bladder control in paraplegia (Brindley *et al.* 1986) by stimulating the roots with natural impulse patterns and

by trying to stimulate more specifically preganglionic motoneurones for detrusor activation (Lullies 1936). The development of a surgical technique for reinnervating the urinary bladder in paraplegic patients by nerve anastomosis is a future step in repairing bladder function (Schalow *et al.* 1992; Schalow and Barth 1992b; Schalow 1992b,c). For further details see Schalow and Barth (1992a).



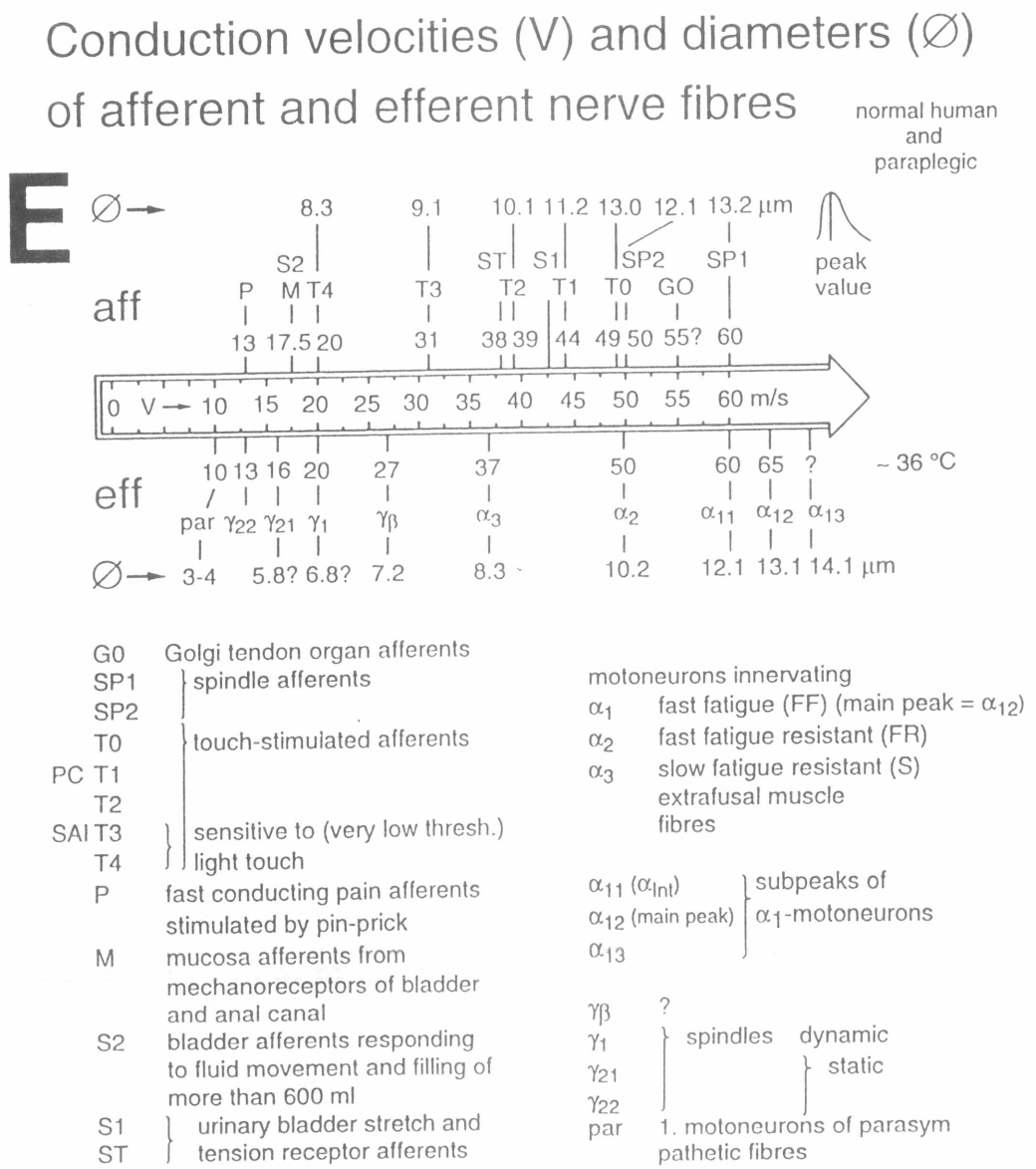


Fig. 1

A. Stimulation and recording layout. Traces "a" and "b" are the records taken from the two sites; downward arrow = efferent, upward arrow = afferent. **B.** Afferent (SP2(5)) and efferent (α_2, γ_1) single fibre action potentials (APs) recorded from the dorsal root S4 of the brain-dead human. The secondary muscle spindle afferent fibre SP2(5) AP is only partly conducted from the recording site "a" to the site "b". **C.** Conduction velocity distribution histograms, calculated from the conduction time and the conduction distance (8 mm), of skin (T0 to T4) and mucosal (M) mechanoreceptor afferents and secondary muscle spindle afferents (SP2). **D.** Conduction velocity distributions of α- and γ-motoneurones on a linear scale (a) and the conduction velocities of the γ-motoneurones additionally on a log scale (b). Designations according to the classification scheme of the human peripheral nervous system (Fig. 1E, Schalow 1991a): α_2-motoneurones innervate fast fatigue-resistant muscle fibres (FR); α_3-motoneurones innervate slow fatigue-resistant muscle fibres (S); γ_1 = dynamic γ-motoneurones; γ_{21}, γ_{22} = static γ-motoneurones; para = preganglionic parasympathetic motoneurones; SP2 = secondary muscle spindle afferents; T0 to T4 = skin mechanoreceptor afferents, M = mucosal mechanoreceptor afferents; probably T1 = PC, T2 = RA, T3 = SAI, T4 = SAII. **E.** Approximate peak values of group conduction velocities (V) (root temperature $\approx$ 36 °C) and group nerve fibre diameters (ϕ) of afferent and efferent nerve fibres in the cauda equina about 3 cm distal to the conus medullaris. Human aged about 30 years. G0, S1, ST, S2, M, γ_{22} = fibre groups with unknown corresponding group nerve fibre diameters, M, S2 = possibly the same afferents. The insert shows the shape of the schematic frequency distribution of conduction velocities and nerve fibre diameters, peak value indicated.

Single fibre action potentials (APs) from lower sacral nerve roots (Fig. 1A) were recorded extracellularly with two platinum wire electrode pairs (electrode pair distance = 8 mm; electrode distance in each pair = 4 mm) at two sites, preamplified (x1000), filtered (RC filter, passing frequency 100 Hz–10 kHz), displayed on a digital storage oscilloscope (Vuko Vks 22-16) and stored using a PCM processor (Digital Audio Processor PCM-501ES) and a video recorder (JVCD 250EG). The active 50 Hz filter was sometimes used between the preamplifier and the oscilloscope or when playing back from the tape between the processor and the oscilloscope.

The trace "a" in Fig. 1 was recorded from the proximal pair whereas the trace "b" from the distal pair of electrodes. Conduction velocities of single fibres with the corresponding APs on the two traces were calculated from the conduction distance (electrode pair distance) and the conduction time from recordings such as that in Fig. 1B. Single fibre APs were always recorded from whole roots or fascicles. Only the arachnoidea connections were cut; no attempt was tried to tease single fibres. In nerve roots thinner than 0.3 mm in diameter (radial decline of AP amplitude is approximately aplitude/10 for 0.3 mm), it is possible to record single fibre APs from all fibres with a diameter larger than 4.5 μm. If only a few of these fibres, up to a few hundred, are active at a time, then it is possible to split the summed activity into single fibre activity. APs from afferent and efferent single fibres could clearly be distinguished since the main phase (second phase) of afferent fibres is upwards and of efferents downwards (Fig. 1A, Fig. 1B trace "b") with the arrangement of our electrodes. Conduction velocity distribution histograms were constructed separately for afferents (Fig. 1C) and efferents (Fig. 1D). Histogram classes were half closed intervals ($\leq$ and $<$); the left border belongs to this class, the one on the right does not. Practical recording aspects are discussed in Schalow and Barth (1992a). By knowing roughly the frequency distribution curve of conduction velocity of a single group in nerve fibres (insertion of Fig. 1E), peak values and the borders between nerve fibre groups were identified (Schalow 1992a). The overlap of group distributions is smaller at higher temperatures (Schalow and Zäch 1994). By correlating the group conduction velocities with the group nerve fibre diameters (peak values) (Schalow 1991a, Schalow and Barth 1992a), a classification scheme for the human peripheral nervous system was constructed (Fig. 1E). With a further research, the still missing fibre groups will have to be included into the new scheme. Nerve fibres can now be identified by their conduction velocity and their nerve fibre diameter. Current knowledge of impulse patterns further helps this identification. Single fibre APs, conducting with the same or similar velocities, can be distinguished from each other by comparing their wave form (Schalow 1991a, 1992c). To separate single unit impulse patterns, the times of occurrence and reoccurrence of the different AP wave forms are registered with the memory address of the oscilloscope. The times of occurrence of, for example, AP wave form 1 are put into fibre class 1 and those of AP wave form 2 into fibre class 2. The times of fibre class 1 and 2 are plotted then below each other for the same time scale as in Figs 2 and 4B. In this way it is possible to separate the impulse patterns of single fibres from the summed activity. It is often possible to separate the patterns of a few single fibres from the complex impulse pattern recorded from the root.

By measuring impulse patterns from single afferent and efferent fibres simultaneously, it is possible to study, in an almost undamaged nervous system, receptor properties of skin, bladder and anal canal afferents, and the responses to afferent activity as well as the natural impulse patterns of motoneurones innervating skeletal and smooth muscles (Schalow 1993d). With the measurement of the afferent input into the spinal cord and the efferent output from the spinal cord, it is further possible to analyse the functions of circuitries of the human central nervous system under normal and pathological conditions (Schalow 1991b, 1993a).

The time intervals were measured from the screen (for example 1 ms/cm) and later by a memory address to enhance accuracy. A discrepancy of 5 to 8 % was found between both methods of time interval measurements. The absolute measured values therefore vary only slightly. Since afferent and efferent APs were always recorded simultaneously and analysed in the same way, this systematic error does not affect the relationship between afferent and efferent activity.

The somatic fibres of the S3 to S5 nerve roots innervate the pelvic floor (S4, S5) and the external anal and bladder sphincters. Muscle spindle afferents thus innervate spindles in these muscles. The external bladder sphincter probably contains no muscle spindles. As verified by conduction velocity and nerve fibre diameter distributions (Fig. 1E, Schalow 1991a), there are no primary spindle afferents (peak group conduction velocity = 60 m/s at 36 °C; peak group diameter = 13.1 μm) in the S5 root, very few in the S4 root, a few in the S3 root and a large number in the S2 root. The primary spindle afferents of the brain-dead humans contained in the S3 and S4 roots showed only little activity. Electrical stimulation of the S2 root, during the implantation of a sacral anterior root stimulator in paraplegics, caused a contraction of the gluteus maximus muscle (L5–S3) (identification sign for the S2 root) and a plantar flexion of the foot. Stimulation of the S3 or S4 roots caused digital flexion of varying strength. The secondary muscle spindle afferents (peak group conduction velocity = 50 m/s at 36 °C, peak group diameter = 12 μm) innervate the

pelvic floor and the external anal sphincter through the S3 to S5 roots and the gluteus maximus and leg muscles through the S2, S3 and S4 roots. The muscle spindles contributing to continence may be innervated differently (perhaps by secondary spindle afferents and parasympathetic fibres besides γ-fibres, see Introduction) than those contributing to locomotion (innervated by primary and secondary afferents and no parasympathetic fibres).

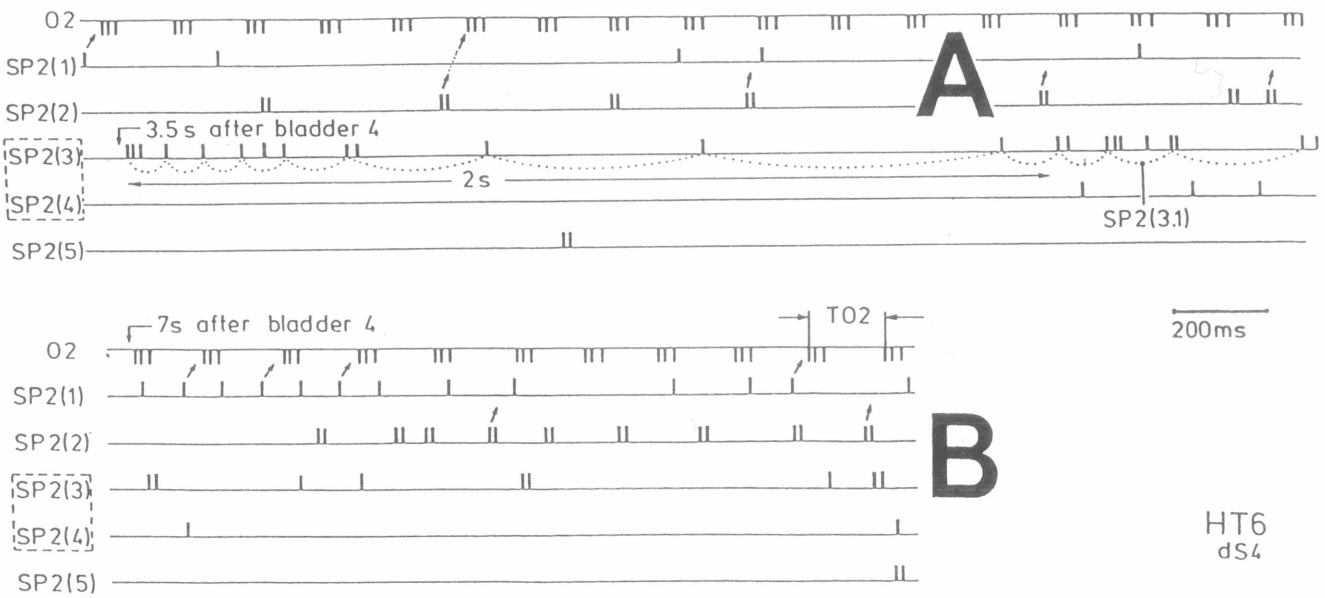


Fig. 2
Impulse patterns of five secondary muscle spindle afferent fibres, SP2(1) through SP2(5), in relation to the impulse pattern of the oscillatory firing α_2-motoneurone O2 following bladder catheter pulling. Bars represent APs. Very short interspike intervals (as in doublets) are not drawn to scale; only the first APs are in their exact position. The dashed rectangle around SP2(3) and SP2(4) indicates that both afferents probably innervate the same spindle; SP2(4) may represent a tertiary fibre because of the slower response to stimuli and a comparably slow conduction velocity. The dotted curves, linking certain APs of the SP2(3) activity, most likely represent the activity from a single ending. The small arrows indicate similar time intervals from the afferent APs to the motoneurone APs (phase relation). TO2 = oscillation period.

Results

Impulse patterns of secondary muscle spindle afferents

From recordings such as Fig. 1B, impulse patterns were constructed for five secondary muscle spindle afferents SP2(1) through SP2(5) and are shown in Fig. 2. For comparison, the activity of the oscillatory firing α_2-motoneurone O2 is included in the set of recordings. The fibres SP2(1) and SP2(4) are also shown in Fig. 2.

Fig. 2 presents activity patterns similar to those recorded from limb muscles (Burke *et al.* 1979). The secondary spindle afferent fibres SP2(2) and SP2(5), and partly SP2(3) in Fig. 2B, fired with doublets with an interspike interval of about 13–16 ms. This doublet firing was partly analysed by Schalow (1993b,d). The SP2(3) fibre shows a burst-like firing following a strong pull on the bladder catheter in Fig. 2A. Assuming that the interspike interval of a single ending of a parent secondary spindle afferent fibre cannot be shorter than about 50 ms, the impulse pattern of a parent secondary spindle afferent fibre can be split into the impulse patterns of single endings. Future research has to show, whether this assumption always holds, since also fusimotor fibres show doublet firing with a very similar doublet interspike interval (Schalow 1993d). Nevertheless, if single endings of parent secondary spindle afferents do not fire with shorter interspike intervals than 50 ms (i.e. at a frequency higher than 20 Hz), the burst-like firing of the SP2(3) fibre could be split into discharges of single endings, which in turn had similar firing patterns as the SP2(1) and SP2(4) fibres measured simultaneously. The burst-like firing of the SP2(3) fibre can therefore be interpreted rather as simultaneous activation of many single endings of the parent spindle afferent fibre SP2(3) following sudden strong natural stimulation. In this case, the stimulation was a strong pull on the bladder catheter.

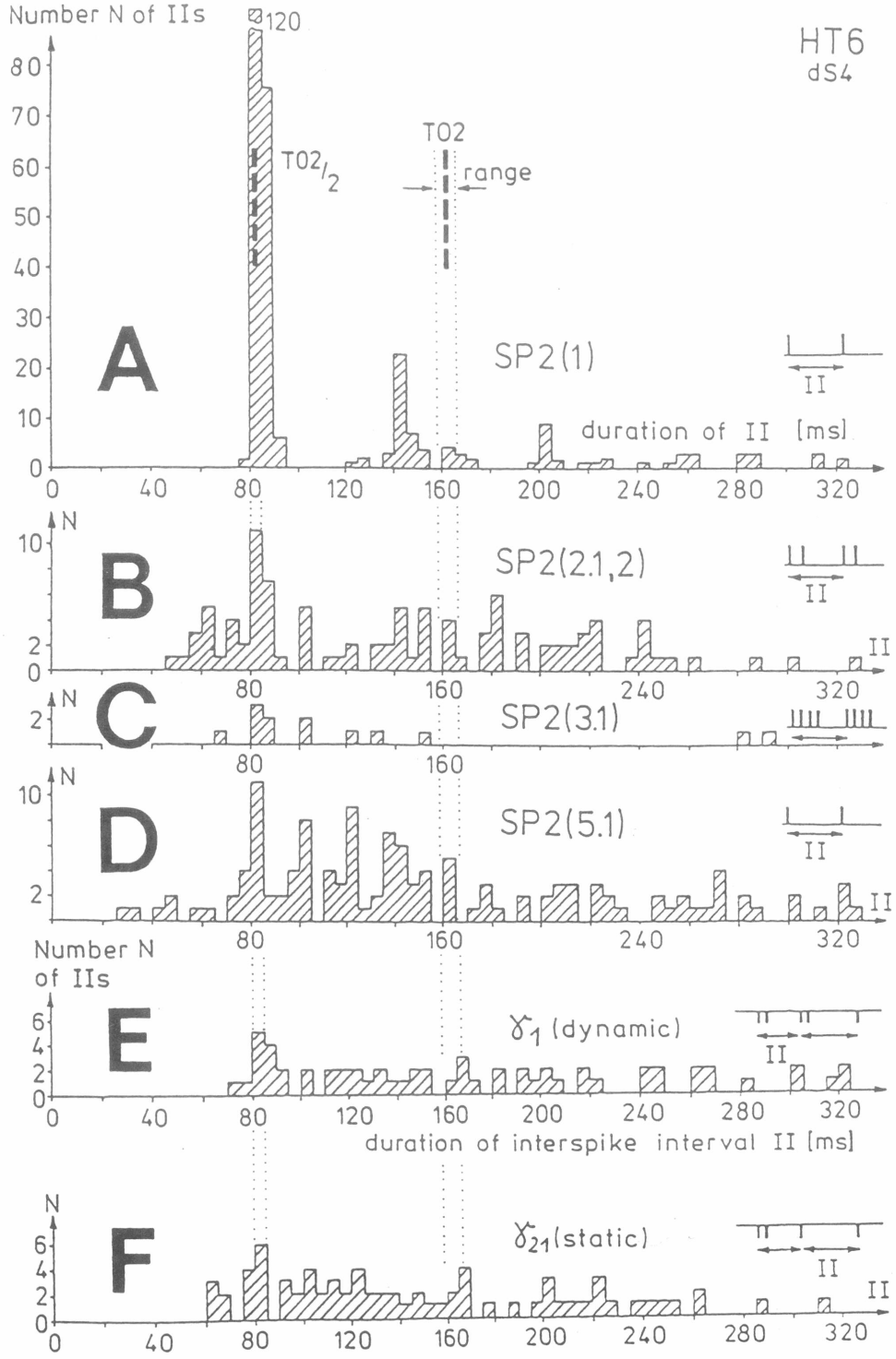


Fig. 3
Interspike interval distributions of single endings of four secondary muscle spindle afferents (SP2) and two γ-motoneurones, measured simultaneously. **A.** The oscillation period TO2 with its range of the simultaneously recorded oscillatory firing α_2-motoneurone O2 is drawn for comparison; also the half of the oscillation period TO2 is indicated. Note that the interspike interval distributions of spindle afferents and γ-motoneurones have the shortest interspike interval, which is nearly identical to a half of the oscillation period. The impulse pattern insections in Figs 3A to 3F show the procedure for measuring the interspike intervals (dS4 root).

Interspike interval distributions of simultaneously measured secondary muscle spindle afferents and α-motoneurones in relation to the oscillation period of an oscillatory firing α_2-motoneurone

Fig. 3 shows the frequency distributions of interspike intervals of four secondary spindle afferents and 2 fusimotor axons recorded simultaneously from the dorsal S4 root of HT6. The oscillation period TO2 and a half of the simultaneously recorded oscillatory firing α_2-motoneurone O2 are indicated by thick bars. It can be seen that the peaks of the shortest interspike intervals are about 80 ms (Fig. 3) for all muscle spindle afferents and efferents and the results correspond to exactly a half of the oscillation period of the oscillatory firing α_2-motoneurone O2. Since muscle spindle afferents and efferents are recorded simultaneously in the same dorsal S4 root, one can expect that the circuitries driving the α_2-motoneurone O2 and the γ-motoneurones and the majority of the projections of the secondary spindle afferents are closely positioned in the S4 segment of the medulla. Since the SP2(1) fibre showed most regular firing at interspike intervals of 80 ms at the time of recording, the SP2(1) fibre probably contributed strongly to the drive of the oscillatory firing of the α_2-motoneurone O2. Since the most frequent secondary muscle spindle affferent interspike interval was 80 ms, which is a half of the oscillation period of TO2, it is likely that the oscillatory system, in which the α_2-motoneurone O2 was integrated (Schalow 1993a), could pick up spindle afferent interspike intervals of half the duration of the oscillaton period (i.e. double frequency), as many mechanical and electronic oscillators can do.

As can be seen from Fig. 3, the γ_1 (dynamic) and γ_{21}-motoneurones (static) fired with similar interspike intervals as the secondary spindle afferents, even though not firing in an oscillatory manner themselves. This could mean that the impulse patterns of the γ-motoneurones are related to the activity patterns of secondary spindle afferents (γ-loop?) or that the circuitry of the central nervous system, driving the γ-motoneurone, is partly connected to the circuitry driving the oscillatory firing α_2-motoneurone O2, or both.

Interspike interval distributions of secondary muscle spindle afferents obtained from root filaments other than the oscillatory firing axon

Fig. 4A shows the recording from a different sacral root filament of the brain-dead human than that recorded in Fig. 3. The two extracellular APs show a different triphasic form on the traces "a" and "b" and can therefore be distinguished from each other. The impulse patterns of the six simultaneously recorded secondary spindle afferents SP2(6) through SP2(11) are drawn in Fig. 4B. The patterns of the fibres SP2(6) and SP2(7) are plotted together to show clearly the similarity of their firing. The APs of the SP2(6) and the SP2(7) fibres are certainly from two different parent secondary spindle afferent fibres (no AP wave form misjudgement), since it sometimes happened that the APs occurred very close to each other, so that the AP amplitudes summated. If the AP wave forms had been misjudged as being from two single endings of the same parent fibre, then one AP would have been cancelled because of running into the refractory period of the other. The half-circle lines connecting impulse bars of the impulse patterns of the fibres SP2(9) and SP2(10) in Fig. 4B mark the activity of single endings.

In Figs 4C to 4H the frequency distribution histograms of the six secondary muscle spindle afferents SP2(6) through SP2(11) are plotted. The distributions are quite different from the oscillation period TO2 of the oscillatory firing α_2-motoneurone O2 or from its half. Only the impulse activity of the secondary spindle afferent fibre SP2(10) could contribute to the excitation of the oscillatory firing α_2-motoneurone O2, since its interspike intervals had a similar duration as one half of the oscillation period.

In comparison to the interspike interval frequency distributions in Fig. 3, the interspike interval distributions in Figs 4C to 4H are more variable with respect to half of the oscillation period TO2. It seems therefore that the circuitry evoking the oscillatory firing of the α_2-motoneurone O2 was rather localized in the medulla. The interspike interval frequency distributions of the SP2(6) and SP2(7) fibres resemble the distributions recorded from arm or leg muscles (Burke *et al.* 1979). The SP2(6) and SP2(7) fibres probably project to motoneurones which are mainly connected to gait or locomotion rather than to continence. The interspike interval frequency distribution of the secondary spindle afferent fibre SP2(12) in Fig. 4I was obtained from a coccygeal root of the brain-dead human HT6. Only one spindle afferent fibre was found in the root. Since the interspike interval distribution range is very similar to the whole oscillation period TO2 range, this secondary spindle afferent fibre could contribute most strongly to the drive of the oscillatory system driving the α_2-motoneurone O2. This points to the fact that the circuitry driving the anal sphincter is situated most caudally in the conus medullaris.

Interspike intervals of stretch receptor afferents of the urinary bladder wall in relation to the oscillation period of the oscillatory firing α_2-motoneurone O1 innervating the external urethral sphincter

Fig. 4L shows the interspike interval frequency distribution histogram of the secondary muscle spindle afferent fibre SP2(13). This fibre could contribute to the drive of the oscillatory firing α_2-motoneurone O2, since its interspike intervals were in the range of 80 ms, which is half of the oscillation period TO2.

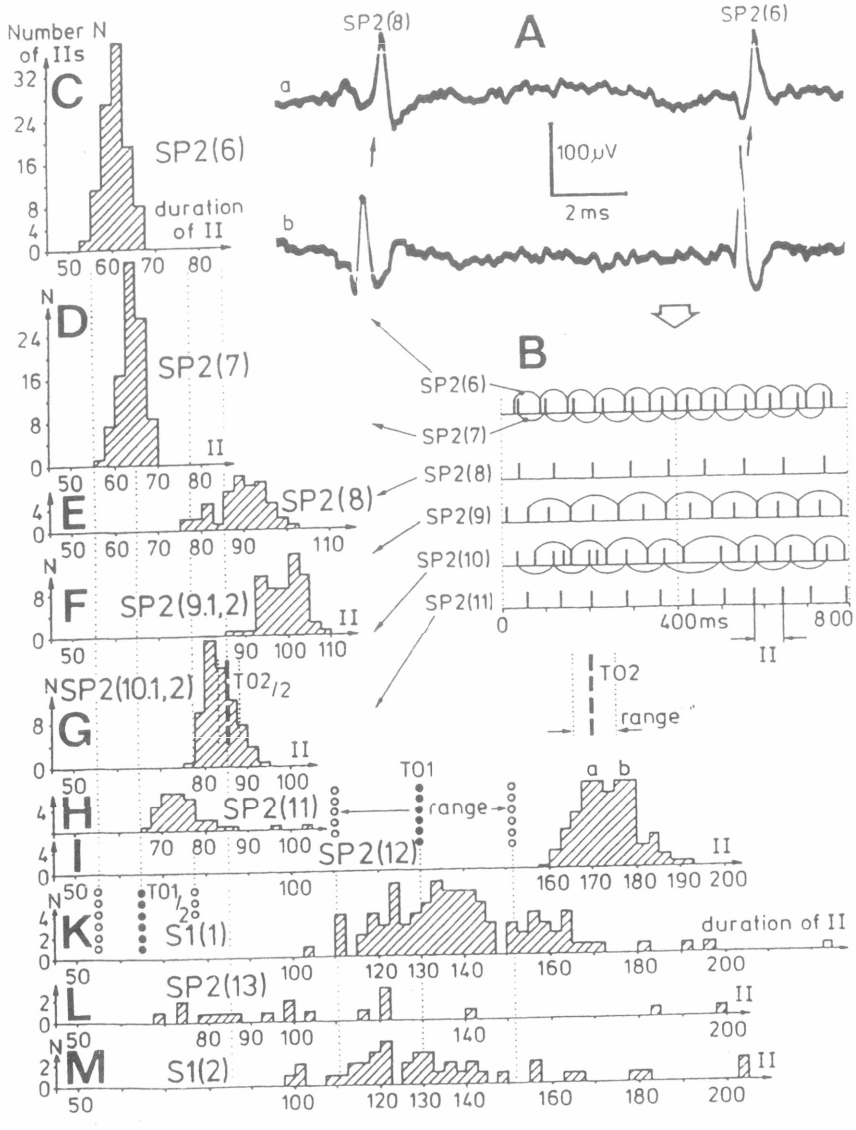


Fig. 4

Measurements from the brain-dead human after retrograde bladder filling (700 to 800 ml), with the exception of Fig. 4I, which was obtained before filling. **A.** A sweep trace of a recording from a dorsal S3 or S2 root filament. It can be seen that the secondary muscle spindle afferent SP2(6) AP can be distinguished by the wave form on the two traces from the secondary spindle afferent fibre SP2(8) AP (different amplitude of the three phases of the triphasic APs). **B.** Simultaneously measured impulse patterns of the six parent secondary spindle afferents SP2(6) through SP2(11) obtained from recordings as in Fig. 4A (dS3 or dS2 root). The impulse patterns of the SP2(6) and SP2(7) fibres are not separated to show the similarity of the patterns. The impulse patterns of the parent spindle afferents SP2(9) and SP2(10) are split into patterns of the single endings (single ending activity partly connected by circle lines) with the assumption that single endings of parent secondary spindle afferents should have interspike intervals of longer duration than 50 ms. **C to H.** Interspike interval distributions of six simultaneously recorded single secondary spindle afferent endings. Figs 4F and 4G show the interspike interval distributions of parent fibres, which are the sums of the distributions from two activated single endings. **I.** Interspike interval distribution of a secondary spindle afferent fibre (SP2(12)) of a coccygeal root. **K, L, M.** Interspike interval distributions of single fibre afferent activity from a lower sacral dorsal root. In Fig. 4L, most likely the afferent activity from a secondary spindle afferent fibre is shown. In Figs 4K and 4M most likely the interspike intervals from afferents (S1(1) and S1(2)), innervating stretch receptors of the urinary bladder wall, are shown. In Figs 4G, 4H and 4K the durations of the oscillations periods (mean and range) of the oscillatory firing α_2-motoneurones are indicated by thick dashed and dotted lines, which innervate the external anal sphincter (TO2) and the external bladder sphincter (TO1). Note the TO1 and TO2 ranges, and their halves which overlap with the interspike interval distributions of the secondary spindle and stretch receptor afferents.

The interspike interval distributions of Figs 4K and 4M show distributions of most likely stretch receptor afferents of the urinary bladder wall, since their interspike interval durations fall into a range which was found previously to be in the range of stretch receptor afferents (Schalow 1991a,b). This interpretation fits into the range of oscillation periods of the oscillatory firing α_2-motoneurone O1. This neurone most likely innervates the external sphincter of the urinary bladder and falls within the ranges of the interspike interval distribution of stretch receptor afferent fibres (S1).

There could also have been urinary bladder stretch receptor afferents in the other root filaments, from which we recorded. But only the activity from the sacral root filament in Figs 4K, 4L and 4M was recorded after filling the urinary bladder retrogradely with up to 800 ml of liquid. It was shown earlier that stretch receptor afferents start to fire when the bladder wall is stretched (Schalow 1991b). We did not try to reconstruct the interspike interval distributions from the root from which we recorded activity during retrograde bladder filling (dS4 root, Fig. 3), because 1) the activity of all the afferents was rather high following bladder filling, so that misjudgements of the AP wave form could occur more easily, and, 2) during the filling process the interspike intervals of the stretch receptor afferents will probably change.

Discussion

Muscle spindle discharge patterns for continence and locomotion

The discharge patterns of secondary muscle spindle afferents (SP2) are shown in Figs 2, 3 and 4. In Fig. 3 the interspike interval patterns are very regular with respect to the shortest interspike interval of 80 ms, but the ranges of the interspike intervals are widely distributed. The fusimotor axons γ1 and γ21 also showed regular firing with respect to the shortest interspike interval and were also present in that S4 dorsal root. On the other hand, Fig. 4 demonstrates the interspike interval distribution of secondary spindle afferents of root filaments one or two segments away from the S4 segment. The interspike intervals of these fibres are much more narrowly distributed. But the distributions of the shortest interspike intervals of different fibres differed markedly. The secondary spindle afferents SP2(6) through SP2(11) in Fig. 4 show narrow interspike interval distributions very similar to those measured in pretibial muscles of healthy human subjects (Burke *et al.* 1979). This similarity is satisfying since it was recorded in both cases from human spindle afferents innervating similar muscle groups (see last section of Methods). The only difference was that Burke *et al.* (1979) recorded from sites close to the muscles whereas we recorded approximately 1 m from the muscles. The muscle spindle afferents in Fig. 3 are therefore probably associated with continence and innervate muscle spindles of the external anal sphincter and the pelvic floor muscles. The muscle spindle afferents in Fig. 4 are most likely connected to gait and locomotion.

For understanding the mechanism of continence, it is therefore necessary to record from muscle spindle and other receptor afferents which contribute to continence. Since it has further been found that the secondary muscle spindle afferents and fusimotor fibres can fire with doublets of about 11–16 ms duration (Figs 2 and 3; Schalow 1993b,d) and that muscle spindles can be innervated by parasympathetic motoneurones (Schalow 1993d), muscle spindles of continence muscles have to be further explored electrophysiologically and morphologically. The electrophysiological measurements have to include simultaneous recording from muscle spindle and urinary bladder afferents, from α- and γ-motoneurones, and parasympathetic motoneurones. Hopefully, recordings from sympathetic fibres are also sometimes possible, since sympathetic fibres innervate the internal sphincter at the bladder neck. It is argued sometimes that they cause the high pressure in reflex bladders of paraplegics (Torrens and Morrison 1987).

Relations between the functional units controlling the continence of urinary bladder and rectum

By comparing the interspike interval distributions of secondary spindle afferents in Figs 3 and 4 with the duration of the oscillation period of the oscillatory firing of α_2-motoneurone O2, innervating the external anal sphincter or functionally closely related pelvic floor muscles, it may be seen that several spindle afferents do not contribute to the drive of the oscillatory firing motoneurone. The two stretch receptor afferents of the bladder wall seem to be connected to the oscillatory firing of the α_2-motoneurone O1 innervating the external bladder sphincter, since their interspike interval values were similar to the range of the oscillation period TO1 of the α_2-motoneurone O1. The more specific drive of external urethral sphincter motoneurones by stretch receptor afferents than that of external anal sphincter motoneurones by secondary muscle spindle afferents is probably due to the fact that the stretch receptor afferents are more specifically connected to the continence of the bladder than secondary spindle afferent fibres to the continence of the rectum. Muscle spindle afferents innervating the pelvic floor not only serve continence functions and some muscle spindle afferents contained in S2, S3 and S4 roots innervate leg muscles and contribute to gait and locomotion.

The functional units for continence of the rectum and of the urinary bladder are quite different with respect to the durations of the interspike intervals

(and oscillation periods) and probably also with respect to the afferent projections. Nevertheless, following a spinal cord lesion and sprouting of afferents to former tract synapses, it cannot be excluded that secondary muscle spindle afferents contribute to the excitation of α_2-motoneurones innervating the external bladder sphincter and bladder stretch receptor afferents to α_2-motoneurones innervating the anal sphincter. If some spinal oscillators became unstable following the spinal cord lesion (due to interneurone cell death) so that the oscillation periods cover widespread ranges instead of a single value (Schalow 1993a), then the interspike intervals of spindle afferents could become transiently similar to the oscillation periods of motoneurones innervating the bladder sphincter and the interspike intervals of the stretch receptor afferents similar to the oscillation periods of the motoneurones innervating the anal sphincter. Under pathological conditions it seems that specific afferents organize and also activate functionally unrelated oscillators so that dysfunction may occur.

It has been reported that afferents do not sprout to former tract synapses in the medulla following spinal cord lesion. The rearrangement and adaptation of the disconnected human caudal medulla needs further consideration, especially since interneuronal cell death can be expected following spinal cord lesion (Nesmeyanova 1977). It may be possible in the future, to measure electrophysiologically human motoneurone synaptic changes at the dendrites and the soma by a reduction of the shortest soma-dendritic spike interval (Schalow 1991b, 1993a).

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Reprint Requests

G. Schalow, M.D., Ph.D., Schweizer Paraplegiker-Zentrum, CH-6207 Nottwil, Switzerland.