Group Conduction Velocities and Nerve Fibre Diameters of α and γ -Motoneurons from Lower Sacral Nerve Roots of the Dog and Humans.

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Abstract. Single action potentials and their conduction times were recorded extracellularly from dog and human lower sacral nerve roots. Conduction velocity frequency distribution histograms were constructed and peaks of single extrafusal and intrafusal motoneuron distributions were identified. The electrophysiologically measured roots were removed and morphometrically analysed. Nerve fibre diameter frequency distribution histograms were constructed with respect to 3 myelin sheath thickness ranges, and peaks of single motoneuron group distributions were identified.

The identified motoneuron classes, characterized by their group peak values of conduction velocity at about 36 °C and fibre diameter were:

dog: intrafusal: $\gamma_{22}(23 \text{ms}^{-1}/4.8 \mu \text{m}), \gamma_{21}(33/5.7), \gamma_1(43/6.7), \gamma_{\beta}?(54/10.1)$ extrafusal: $\alpha_3(61 \text{ms}^{-1}/11.7 \mu \text{m}), \alpha_2(72/13.6), \alpha_{11}(81/15.2), \alpha_{12}(86/16.8), \alpha_{13}(95/19)$

human: intrafusal: $\gamma_{21}(15\text{ms}^{-1}/5.8\mu\text{m}), \gamma_1(20/6.8), \gamma_{\beta}?(27/7.2)$ extrafusal: $\alpha_3(37\text{ms}^{-1}/8.3\mu\text{m}), \alpha_2(50/10.2), \alpha_1(60/13.1)$

The 60 (α_3) to 30% (α_1 -motoneurons) higher conduction velocities in dogs as compared to humans seem to originate in the 40 (α_3) to 30% (α_1 -motoneurons) larger nerve fibre diameters. However, the myelin sheath seemed to be 0.1 to 0.2 μ m thinner in dogs than in humans.

The pair-values "conduction velocity - fibre diameter" of the α and γ -motoneuron groups were lying on different correlation curves in the velocity-diameter plane indicating structural and/or geometrical differences between α and γ -motoneurons.

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Introduction

The present research in basic clinical neurophysiology is aimed at developing a surgical technique to partly cure spinal cord lesions and to restore urinary bladder function (Schalow 1985, 1989, 1991b, Schalow et al 1987) in paraplegia The concept includes establishing a nerve anastomosis from the intercostal nerves rostral to the level of lesion to the lower sacral nerve roots, which originate in the lower spinal cord (Schalow 1985, Schalow et al 1987, Schalow 1991b) A similar reconnection of nerve fibres requires a detailed knowledge of the nerve fibre group compositions of the intercostal nerves, the pudendal nerve, the pelvic nerves, the hypogastric nerve and the sacral nerve roots During the surgery, nerve roots have to be identified both anatomically (Schalow 1985) and functionally (Schalow and Lang 1987) The representation of the urinary bladder innervation in the nerve roots and the bladder function have to be distinguished as perfectly as possible during the surgery The analysis of the nerve fibre group composition of the nerves innervating the bladder and splitting up of the single fibre action potential traffic in the nerve roots (afferent and efferent fibre groups) requires a precise and detailed morphological and electrophysiological basis for the identification of nerve fibre groups Since frequently only electrophysiological measurements are possible (intraoperative diagnosis) and sometimes only morphometry of nerve fibres (autopsy), a nerve fibre group classification is needed which would allow identification of nerve fibre groups morphometrically and electrophysiologically A similar classification scheme started developing (Schalow and Lang 1989, Schalow 1989, 1991a, b, c) based on electrophysiologic and morphometric measurements on brain-dead humans Since there is evidence that the efferent nerve fibre groups belong to motoneurons with different functions in the spinal cord (Schalow 1991b), and to avoid confusion with other classification schemes, the efferent fibre groups will further be designated by their respective motoneuron type A detailed analysis of peripheral nerve impulse traffic under conditions of physiological stimulation will be possible with the new classification scheme being extended to so far unidentified fibre groups, also, this would require an enhancement of the accuracy of the peak values and of the ranges of conduction velocities and fibre diameters of the fibre groups A similar improvement can additionally be achieved in animal experiments if exactly the same method is used for the measurements

In a series of three papers in this volume values of single fibre action potential and fibre diameter measured in dogs are compared with those obtained in humans. These measurements were aimed at improving the method for the use in humans, to provide animal reference data, and to reveal differences in the sacral roots and sacral spinal cord between dogs and humans. In the first paper conduction velocities and fibre diameters of nerve fibre classes are compared. The second paper deals with the activities of the different motoneuron classes, and recruitment within motoneuron classes, upon physiological stimulation. In the third paper, activity increases following natural stimulation of afferents will be compared with those of efferents.

In this first paper peak values of group conduction velocities of myelinated efferent nerve fibre classes will partly be correlated to the peak values of their group fibre diameters of measured distributions. Nerve fibres will be classified in dogs and humans based on paired values of peak group conduction velocities and peak group nerve fibre diameters instead of using the A, B and C system of Erlanger and Gasser (1937), or the I to IV group system of Lloyd (Lloyd 1943; Boyd and Davey 1968). This work continues earlier papers which described the method of single fibre action potential (AP) recording in human nerve roots (Schalow and Lang 1989; Schalow 1989; 1991a) and correlated conduction velocities with nerve fibre diameters of motoneurons (Schalow 1989; 1991a). The efferent conduction velocity and fibre diameter distributions in the dog are better suited to identify human distributions since in the dog there are less afferents in the lower sacral nerve roots (Schalow 1992b) than in human (Schalow 1989), thus influencing to a lesser degree the typical fibre diameter distributions of the efferents.

Materials and Methods

Methods were described in a previous publication (Schalow 1991a). Data were obtained from measurements in 2 dogs (Alsatian) and 2 brain-dead humans (Hirntote=HTs). The dogs were anaestesized with 250 Ketamine i.m. $(+(N_2+O_2))$, and blood pressure in HTs was kept by the administration of Dopamine $(4\mu g/kg \text{ per min})$, as in kidney removals.

Ethics

The measurements were done in accordance with the Helsinki Declaration, and were performed to reconstruct urinary tract function as in kidney removals. The measurements on HTs, serving the development of a surgical technique in paraplegia, were approved by the Ethical Committee of the GDR. In Germany (80,000,000 inhabitants) the number of paraplegics increase by approx. 1 300 yearly. About 130 of them commit suicide because of the "no hope" situation. Others die because of high pressure and infections in the urinary bladder, and the remainder live although their quality of life is low.

To clarity, as soon as the Committee decides that the patient is brain-dead, the patient is considered as a cadaver and no more as a patient. Mostly, cadavers are transferred to urology department for kidney explantation or, after switching off the respirator, the cadaver is transferred to the pathology department for autopsy. From the anatomical viewpoint, it is an honour to the former human if his cadaver is of essential benefit to the society, instead of just being metabolized or eaten by lower species. Animal experiments are necessary for basic clinical research. However certain knowledge cannot be obtained from animals and why killing animals if in some cases more relevant knowledge can be obtained from human cadavers?



Figure 1. Schematic representation of the recording of extracellular single fibre action potentials from a bundle of 7 nerve fibres. Drawing not to scale. A. The afferent nerve fibres 1, 2 and 3 and the efferent fibre 4 are occasionally active as indicated by the arrow and the single unit potential; fibres 5, 6 and 7 are not active. Large single unit potentials from thick fibres are indicated by large potential changes and small ones by small potential changes. B. Traces I (1 to 7) show the theoretical recordings of the single fibres. Trace II shows the arithmetic sum of the 7 recordings. C. Trace I shows the noise and artefact background levels, II is the constructed recording (sum of traces II (B) and I (C) of 3 single unit potentials from 3 nerve fibres in a bundle of 7 nerve fibres. The potential of fibre 2 is lost because of a low amplitude. D. Stimulation and recording lay out. The figures at the single unit potentials correspond to the nerve fibre numbers in A, B and C. Traces a and b are the records taken from the 2 sites; downward arrow (4)=efferent, upward arrow (3,1)=afferent. The stimulations used were touch, pin-prick, anal and bladder catheter pulling.

Electrophysiology

Action potentials (APs) from nerve roots (Fig. 1) were recorded extracellularly with 2 platinum wire electrode pairs (electrode pair distance=8mm; electrode distance in each pair=4mm) at 2 sites, pre-amplified (x1000), filtered (RC-filter, passing frequency range 100Hz-10kHz), 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 (JVC-Kasettenrecorder, Modell Nr. Hr-D250EG). A sharp 50Hz filter was sometimes used between the pre-amplifier and the scope or when playing back from the tape between the processor and the scope. Trace "a" was the recording from the proximal pair and trace "b" from the distal pair. Conduction velocities of single fibres were calculated from the

conduction distance (electrode pair distance) and the conduction times (Fig. 2). Conduction velocity frequency distribution histograms were constructed. Histogram classes were \leq and <.

Practical aspects: Since nerve roots have no epineurium and nearly no perineurium (Schalow 1989), the nerve fibres in the roots can easily be alterated mechanically when recording with wire electrodes. Pressure and stretch will change the action potential (AP) wave form or even block the conduction so that an AP can be recorded from one electrode pair only. Double peaked APs can occur probably when a node of Ranvier is blocked. Stretch of the roots has to be avoided as much as possible and pressure can be reduced by having a very small drop of saline solution (0.9% NaCl) at each wire electrode. Heavily distorted APs from alterated fibres have to be omitted from the analysis. APs of large amplitude cause by shunt a deflection on the other trace and deepen in this way the first or the third phase of the extracellular triphasic AP. This artificial deflection may be abolished by increasing the distance of the electrodes. Distances between the electrodes were not increased because quite often the space is scarce and the electrode arrangement should always be the same to standardize the recording conditions. A false plugging of the wire electrodes can change the AP waveform. With the recording of touch activity (Schalow and Lang 1989; Schalow 1989, 1991a) it can easily be proved that the wiring is correct. The advantage of the recording with wire electrode pairs is that no Faraday cage (normally not available in operating theaters) is needed, which is an important point in this new recording technique. For monopolar recording additional screening is needed. Exact measurement of the temperature of roots remains a problem. Paraffin oil cannot be used during surgery. With the simultaneous recording of afferents and efferents, conduction velocity distribution histograms can be calibrated since in humans the α_2 motoneurons (fibres) conduct with the same velocity as do the secondary spindle afferents, and 10% faster than the T1 skin afferents (probably innervating Pacinian corpuscles) (see Fig. 3 in Schalow 1991a). It is easy to identify APs with a large amplitude to measure conduction times. APs with small amplitudes are more difficult to identify. Since on the average the AP amplitude correlates to the AP duration and the conduction time (Fig. 3 in Schalow 1987; Schalow and Lang 1989), the experienced eye needs but a short training to recognize low amplitude APs. - The group diameter (peak value) of preganglionic parasympathetic fibres (about $3\mu m$) (Fig. 8 in Schalow 1989) is smaller than those of the large γ -motoneurons (4 to 7μ m in average). The myelin sheaths of the parasympathetic fibres are also thinner. The APs of parasympathetic fibres could therefore not be identified as yet. The recording conditions at the roots, the techniques of sweep digitalization, and conduction time measurement can still be improved. It seems therefore likely that the APs of parasympathetic fibres will occasionally also be made visible in the future. Sympathetic fibres leave the spinal cord at the thoraco-lumbar level. Ventral root afferents and dorsal root efferents have been demonstrated in the human lower sacral nerve roots (Schalow 1989; 1991a). Occasional reflection of an AP at the motoneuron soma, the ganglion branching or at fibre sites where the recording electrodes are positioned cannot be excluded. Most artificial APs occur as the roots dry up. As a result of such an unphysiologic conduction specific properties of the impulse traffic are lost. For example, specific peaks in conduction velocity distribution histograms disappear. The impulse patterns of motoneurons in the oscillatory firing mode are very characteristic independent of whether the axons lead through the dorsal or the ventral roots (Schalow 1991b). Primary afferent depolarization may induce an efferent-like AP to occur in an afferent fibre. Dorsal root potentials are evoked by electrical stimulation of the root, i.e. by

unphysiologic stimulation. The present research has been focused on the impulse traffic in intact human nervous system following physiologic stimulation. Furthermore, following the same physiologic stimulation (e.g. touch), in an HT, different dorsal roots showed different percentages of efferent APs (Schalow 1991a). The coccygeal root contains no efferent fibres, probably because it originates in the conus medullaris below the level of the motoneuron pools. A real progress in this new method for the research and intraoperative diagnosis (Schalow and Lang 1987) came from recordings from the lower human sacral nerve roots, which are thin, long (Schalow 1985), have a good blood supply (Schalow 1990), and have dorsal root efferents (Schalow 1991a) and ventral root afferents (Schalow 1989). Also, the combination of electrophysiology with morphometry of the same roots provided additional important knowledge (Schalow 1991a).

Morphometry

Root pieces of a few centimeters were removed after recording, fixated for 2 to 4 hours in 4% glutaraldehyde in cacodylate buffer, afterfixated in 1% OsO₄ for 2 hours, dehydrated and embedded in Araldite according to standard techniques. Semi-thin sections stained with thionin and acridine-orange were inspected under a light microscope (×1000). Nerve fibre diameters $\emptyset = 1/2(\emptyset_1 + \emptyset_2)$ (\emptyset_1 and \emptyset_2 are the larger and the smaller diameter of non-round-shaped fibres) and the mean myelin sheath thickness, d, were measured by hand. The values were corrected for shrinkage (8%). The values measured for the nerve fibre diameters were grouped into 4 ranges of myelin sheath thickness (0.25 < d0.8; $0.8 \le d < 1.3$; $1.3 \le d < 1.8$; $1.8 \mu m \le d < 2.3 \mu m$).



Figure 2. A. Single fibre action potentials (APs) from a lower ventral sacral nerve root of dog 2. The conduction times and the corresponding velocities are indicated. The APs are labelled according to the group they belong to, based on the conduction velocity histogram in B. Note that the AP amplitude increases from γ_{21} -AP to α_{13} -AP. B. Conduction velocity frequency distribution histogram of a sweep of 0.2 s duration of efferent APs shown in A. The distribution peaks are labelled according to the respective groups they most likely represent. The figures below the group names are the values of the peak conduction velocities for each group. α =extrafusal, γ =intrafusal, γ_{B} =?

Results

Measurements in dogs

Electrophysiology

Action potentials (APs) of a sweep piece of a typical sacral ventral root recording, 2 s following stimulation, is shown in Fig. 2A. The conduction velocities of the single nerve fibre APs were calculated and a conduction velocity frequency distribution histogram of a sweep of 0.2 s duration was constructed (Fig. 2B). In accordance with earlier measurements in humans (Schalow 1989) the peaks were identified with the nerve fibre class to which they most likely belong. The peak values of the different extrafusal (α) and intrafusal (γ) motoneuron group distributions are indicated in Fig. 2B. The APs in Fig. 2A were identified with the motoneuron class they belong to, based on the velocity ranges (for more details see Schalow 1992a) of the motoneuron classes (Fig. 2B) and on the respective conduction velocities.

The α_1 -motoneurons ($\alpha_{11} = \alpha_{int}, \alpha_{12}, \alpha_{13}$) supply fast fatigue muscle fibres, the α_2 -motoneurons fast fatigue resistant, and the α_3 -motoneurons slow fatigue resistant muscle fibres (Burke 1967; Burke et al. 1971; Desmedt 1983; Schalow and Lang 1989; Schalow 1989; 1991a). The γ_1 -motoneurons are dynamic intrafusal motoneurons, and the γ_{21} -motoneurons are static, or one component of static, intrafusal motoneurons. The properties of the γ_{22} -motoneurons are not known. Also, the properties of the γ_{β} -motoneurons remain unknown. As can be seen from Fig. 2A, the AP amplitudes increase from the γ_{21} through the γ_1 up to the α_1 -motoneurons. The separation of of the fused peaks of the γ_1 and γ_{21} -motoneurons will be analyzed elsewhere (Schalow 1992a).

Morphometry

A part of the cross-section of the electrophysiologically measured nerve root (Fig. 2) is shown in Fig. 3A. The nerve fibre diameters were measured from the cross-section, and nerve fibre diameter frequency distribution histograms were constructed for different myelin sheath thickness ranges (d) (Fig. 3B). The peaks were identified with the nerve fibre class they most likely belong to, in accordance with earlier measurements in humans (Schalow 1989; 1991a). The peak values of the different motoneuron distributions are given in Fig. 3B. Note that the γ_{21} and γ_1 -motoneurons are very close to each other (5.7μ m and 6.7μ m), and their myelin sheath thickness is within the same range (0.8μ m $< d < 1.3\mu$ m), whereas the γ_{22} -motoneurons (4.8μ m) have thinner myelin sheaths (0.25μ m $< d < 0.8\mu$ m). Since the conduction velocity depends on the axon diameter and the myelin-sheath thickness, in addition to membrane properties, it is likely that the conduction velocity peaks of the γ_{21} -motoneurons are close to each other (Fig. 2B, and Fig. 1 of Schalow 1992, whereas the γ_{22} -peak is clearly separated from the γ_{21} -peak.



Figure 3. A. Portion of the cross-section of the ventral sacral nerve root measured electrophysiologically (Fig. 2). Thionin acridine-orange staining, contrasted with a copying-machine Minolta 450 zoom. B. Nerve fibre diameter frequency distribution histograms from the light microscope cross-section shown in A. Myelin sheath thickness range d of fibres are given at each column. Distribution peaks are labelled according to the group they most likely represent. The figures below the group names are values of the peak diameter for each group. α =extrafusal, γ =intrafusal, γ_{β} =?



Figure 4A. Relation of the peak values of the group conduction velocity and the group nerve fibre diameter at about 32 °C; dog 2 The respective pair values were taken from Figs. 1 and 2 V/\emptyset =conduction velocity/fibre diameter The velocity-diameter correlation curves are extrapolated to 36 °C (dotted lines)



Figure 4B. Relation of peak group conduction velocity and peak group nerve fibre diameter at 36 °C; human tissue.

Correlation of conduction velocity with the nerve fibre diameter in dogs

In Fig. 4A conduction velocities are plotted against nerve fibre diameter; the peak values of the group conduction velocity (Fig. 2) and the corresponding diameter values (Fig. 3) were used. The conduction velocity - fibre diameter pairs are connected by lines to show trends. It seems that α -motoneurons (extrafusal) lie on a curve different from that for the γ -motoneurons (intrafusal). This may indicate that γ and α -motoneurons have different properties. It also appears from Fig. 4A that the γ_{β} -motoneurons might be more related to the α than to the γ motoneurons. The solid line represents the velocity to diameter correlates for the measured nerve root at approx. 32°C. With a correction factor of 3.5 to 4% per °C (Buchthal and Rosenfalck 1966; Paintel 1973) for the fastest velocities, (dotted line); and using the same velocity shift for the small values (Schalow 1991a), the



Figure 5. A. Extracellular APs from a S4 human dorsal root. B. Conduction velocity frequency distribution histogram of the efferent APs shown in A. 30 sweeps of 1.2 s duration were used. Motoneuron velocity ranges are indicated, together with the peak velocity values. Other details as in Fig. 2.

approximate velocity-diameter dependence for approx. 36 °C is obtained according to it, the velocity is more than 5 times the diameter value.

Measurements in humans

Electrophysiology

Efferent action potentials (APs) of a dorsal root recording are shown in Fig. 5A. The corresponding conduction velocity frequency distribution histogram is shown in Fig. 5B. The velocity values of the different motoneuron classes are indicated below the histogram, and the respective conduction velocities are indicated. The APs in Fig. 5A are identified with the fibre group they belong to, based on the conduction velocities. Even though on average the α_2 -motoneurons have a larger AP amplitude than the α_3 -motoneurons (Schalow and Lang 1989) the AP of the α_3 -motoneuron in Fig. 5A has a larger amplitude than does the α_2 -motoneuron. The quality of the recording was insufficient to enable identification of γ_{22} -motoneurons of very low AP amplitudes.

Morphometry

A part of the cross-section of the electrophysiologically measured dorsal S4 root (Fig. 5) is shown in Fig. 6A. The corresponding nerve fibre diameter frequency distribution histogram is shown in Fig. 6C. Since this was a dorsal root there are more afferents than dorsal root efferents in this histogram. To be able to approximately identity the motoneuron peaks, the histogram of a ventral S3 root of the same HT is given in Fig. 6B. In a human ventral S3 root there are only few afferents (Schalow 1991a). With the peak identification of Fig. 6B, the motoneuron peaks could also be roughly identified in Fig. 6C. Again, the γ_{21} and the γ_1 -motoneuron peaks lie close to each other, with the myelin sheath thickness ranging between 0.8 and 1.3μ m; probably, this results in the fusion of their conduction velocity peaks (Fig. 5B). Probably, the peak of the γ_{22} -motoneurons ($0.25\mu m \leq d < 0.8\mu$ m) is overlapped by the peak of parasympathetic fibres (Schalow 1989) (not shown).

Correlation of conduction velocity with the fibre diameter in humans

To plot the velocity-diameter dependence (Fig. 4B), peak values of group conduction velocities were taken from Fig. 5 and from Schalow 1991a. These were corrected for 36 °C (Schalow 1991a), and peak values of group nerve fibre diameters were taken from Fig. 6 and Table 1. It may seem from the shapes of the curves in Fig. 4B that γ -motoneurons have a velocity-diameter dependence different from that for α -motoneurons, suggesting different properties of extrafusal and intrafusal motoneurons. As for the dog, the γ_{β} -motoneurons seem to belong to the α type rather than to the γ -motoneurons. Since the γ and α -motoneuron velocity-diameter dependences for humans (Fig. 4B) and dogs (Fig. 4A) differ in their mutual relation, it may be that the γ_{21} and γ_1 -motoneurons in humans have



Figure 6. A. Part of the cross-section of the S4 human dorsal root, measured electrophysiologically (Fig. 5). B.,C. Nerve fibre diameter frequency distribution histograms from a ventral S3 human root (B) and from the cross-section, partly shown in A (C). Other details as in Fig. 3.

on the average still slightly smaller peak nerve fibre diameters. In Fig. 4B this is indicated by the arrow.

Comparison of the velocity-diameter dependences for dogs and humans

A comparison of Fig. 2 with Fig. 5, Fig. 3 with Fig. 6, and Fig. 4A with Fig. 4B, shows that the conduction velocities, the fibre diameters, and the velocity-diameter dependences for dogs and humans are similar. As can be seen from Table 1, the differences concern details, and can be understood. Higher maximal conduction velocities were measured for dogs than for humans. The first reason for the higher velocities in dogs could be that there more often is a α_{13} -motoneuron group present in dogs (dog 2, Table 1), which has a very large group diameter (19 μ m). Another more general reason is that the values of the group diameters in dogs are higher than those in humans: 37 (α_3) to 26% (α_1) larger values were measured for dogs than for humans. The corresponding group conduction velocities were 60 (α_3) to 30% (α_1) higher. Since there are many approximations in this comparison, the

Case	Root temp [°C]	Root	Pec 822	1kgr δ ₂₁	oup 84	con [m/s] ອັງ	duct] ∞3 (SP2)	'ion ∝₂ {GO)	velo ¤11 (SP1)	City ∝₁₂	α ₁₃	Peo V22	akg: ∛≩₁	roup វរ	ner [µ ¥ø	ve f m] X3	ibre α ₂	diar X11 X11	nete α ₁₂	Г О(13	Root Ø [mm]
dog 2 f,25kg	32 34	vS3? dS?	15	21	25	36	49 (58)	59 (71)	68 (82)	73	82	48	57	67	101	117	136	15 2	16 8	19	03
dog 4 m 22kg	32	v\$3?	12	17	22	36	43	57	63	-	-	42	52	61	97	11 2	127	15 2	P 16 2	° -	0 25
	34	vs?	14 (1	25 8)	30	515	59 (57)	71 (71)	81 (82)	88	-										
	34	dS?			33	-46	(57)	(71)	(83)	88											
human HT6 f37		v53											62	72	727	82	102	12 3	13 2	2	
	33	dS4) (1	11 2)	14	28?	35 (43)	41 (-)	52 (-)	-	-		58	68	727	82	10 2	12 2	-	-	02
human HT7 m53	32	v\$4				13	18	28	Ĺ	.4			53	63	7 2	283	10 2	12 3	13 1	-	0 25
human (Schal	36			15	20	27	37 (50)	50	60)	50			582	687	72	283	102	121	131	2	

Table 1. Peak values of group conduction velocities and the corresponding group nerve fibre diameters of 2 dogs and 2 female HTs read from histograms similar to those shown in Figs. 2, 3, 5 and 6. The values relate to efferents, those in the round brackets refer to afferents. γ_{22} , γ_{21} , γ_1 =intrafusal motoneurons; γ_β =?; α_3 , α_2 , $\alpha_{11} = \alpha_{int}$, α_{12} , $\alpha_{13} =$ extrafusal motoneurons. SP1, SP2=primary and secondary spindle afferents; GO=Golgi tendon organ afferents, M=touch afferents from the mucosa of the urinary bladder or the anal canal. (-)=no peak present. f=female; m=male; the figures following f and m are age in years; root temp=approximate nerve root temperature; v=ventral; d=dorsal; S=sacral; vS?=ventral sacral root, segment uncertain; Ø=diameter. The afferents were taken from Schalow 1992b for the sake of comparison.

actual values of conduction velocity should not be overly stressed. Nevertheless, the higher group conduction velocities in the dog may mainly be due to the larger group fibre diameters of the α -motoneurons. Although not measured in detail, the human α -motoneurons seem to have by 0.1 to 0.2μ m thicker myelin sheaths than do the dog α -motoneurons. This may mean that to increase the conduction velocity the human α -motoneurons tried to partially compensate for the thinner diameter by a thicker myelin sheath.

The group conduction velocity of the γ -motoneurons (Table 1) is higher for dogs than for humans, whereas there is no difference in the group fibre diameter Since in humans there are quite a lot of afferents in the lower ventral sacral roots,

and efferents in the lower dorsal sacral roots (Schalow 1989; 1991a), the values of the group fibre diameters of the human γ -motoneurons are less exact.

Discussion

Human motoneurons have already been classified based on the conduction velocity - fibre diameter correlation (Schalow 1989; 1991a). In this paper human and dog motoneuron classes are compared in the conduction velocity - diameter plane. The knowledge of the parameters of dog intrafusal motoneurons helped to further improve the values for human γ -motoneurons. The velocity-diameter plots of α and γ -motoneurons seem to differ (Figs. 4A, B) rather than being similarly (Schalow 1991a). This suggests that α and γ -motoneuron fibres differ from each other, and probably this cannot be explained by geometrical differences alone. Unclear is also whether the γ_{β} -motoneurons belong to the class of α or to that of γ -motoneurons.

The axon diameter of motoneurons may decrease along to the muscle. The group diameters of the individual classes of motoneuron fibres therefore only hold for the roots in the spinal canal at 2 to 3 cm from the spinal cord. In humans, the motoneurons run to the sphincters and the pelvic bottom muscles. These muscles are at similar distances from the medulla, and the motoneuron group diameters are useful. In the dog, distances between the spinal cord and the innervated groups may not be very similar, since more different muscles are innervated, including the tail. It is assumed here that the reduction of the axon diameter when going distal is small. Obviously the reduction of fibre diameter in distal parts will have to be estimated.

The conduction velocity of nerve fibres depends strongly on temperature, and since the APs were not recorded at 36 °C, the absolute group velocities are quite approximate. More recordings taken under temperature controlled conditions are needed. Bathing the nerve roots in paraffin oil is not the solution since no paraffin oil can be used in surgery, and —in addition— paraffin oil changes the excitability of membranes (Hodgkin 1948).

The value of recording APs from single nerve fibres in undamaged nerve roots lies in that it allows simultaneous identification of many afferent and efferent nerve fibres and studying of their activity changes down to single fibre activity changes (Schalow 1991a; 1991b; 1991c). Also distinguishing between dorsal and ventral roots is possible during surgery, and dermatoms can be identified in the roots (Schalow and Lang 1987). Impulse patterns of motoneurons (Schalow 1991b) will provide information about the functional stage of the spinal cord, and this may be of significance for the understanding and diagnosis of spasticity. Intraoperative diagnosis of this kind will be of importance in reconstruction neurosurgery.

References

- Boyd I. A., Davey M. R. (1968): Composition of Peripheral Nerves. Livingstone, Edinburgh
- Buchthal F., Rosenfalck A. (1966): Evoked potentials and conduction velocity in human sensory nerves. Brain Res. 3, 1-122
- Burke R. E. (1967): Motor unit type of cat triceps surae muscles. J. Physiol. (London) 193, 141-160
- Burke R. E., Levine D. N., Zajak F. E. III, Tsairis P., Engel W. K. (1971): Mammalian motor units: physiological-histochemical correlation in three types in cat gastrocnemius. Science 174, 709-712
- Desmedt J. E. (1983). Size principle of motoneuron recruitment and calibration of muscle force and speed in man. In: Advances in Neurology, Vol. 39, Motor Control Mechanism in Health and Disease (Ed. J. E. Desmedt) pp. 227-251, Raven Press, New York
- Erlanger J., Gasser H. S. (1937): Electrical Signs of Nervous Activity. Philadelphia, University of Pennsylvania Press
- Hodgkin A. L. (1948): The local electrical changes associated with repetitive action in a non-medullated axon. J. Physiol. (London) 107, 165-181
- Lloyd D. P. C. (1943): Neuron patterns controlling transmission of ipsilateral limb reflexes in cat. J. Neurophysiol. 6, 293-315
- Paintel A. S. (1973): Conduction in mammalian nerve fibres. In: New Developments in Electromyography and Clinical Neurophysiology (Ed. J. E. Desmedt) pp. 19-41, Vol. 2, Karger, Basel
- Schalow G. (1985): The problem of cauda equina nerve root identification. Zbl. Neurochir. 46, 322-330
- Schalow G. (1987): Single unit potential amplitude in relation to the conduction velocity in frog and human. Zbl. Neurochir. 48, 109-113
- Schalow G. (1989): Efferent and afferent fibres in human sacral ventral roots: basic research and clinical implications. Electromyogr. Clin. Neurophysiol. 29, 33-53
- Schalow G. (1990): Feeder arteries, longitudinal trunks and arterial anastomosis of the lower human spinal cord. Zbl. Neurochir. 51, 181–184
- Schalow G. (1991a): Conduction velocities and nerve fibre diameters of touch, pain, urinary bladder and anal canal afferents and α and γ -motoneurons in human dorsal sacral roots. Electromyogr. Clin. Neurophysiol. **31**, 265–296
- Schalow G. (1991b): Oscillatory firing of single human sphincteric α_2 and α_3 -motoneurons reflexly activated for the continence of urinary bladder and rectum. Restoration of bladder function in paraplegia. Electromyogr. Clin. Neurophysiol. **31**, 323–355
- Schalow G. (1991c): Coactivity of secondary spindle afferents and α_2 , α_3 , γ_1 and γ_2 motoneurons innervating anal and urinary bladder sphincters in humans. Electromyogr. Clin. Neurophysiol. **31**, 223–241
- Schalow G. (1992a): Recruitment within the groups of γ_1 , α_2 and α_3 -motoneurons following urinary bladder and anal-catheter pulling in dogs and humans. Gen. Physiol. Biophys. **11**, 101–121
- Schalow G. (1992b): Ventral root afferent and dorsal root efferent fibres in lower sacral nerve roots in dogs and humans. Gen. Physiol. Biophys. 11, 123-131
- Schalow G., Aho A., Lang G. (1987): Nerve fibre counts for an intercostal nerve to cauda equina nerve root anastomosis. Zbl. Chir. 112, 457-461

- Schalow G., Lang G. (1987): Recording of single unit potentials in human spinal nerve roots: a new diagnostic tool. Acta Neurochir. 86, 25–29
- Schalow G., Lang G. (1989): Electrodiagnosis of human dorsal sacral nerve roots by recording afferent and efferent extracellular action potentials. Neurosurg. Rev. 12, 223— 232

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