Recruitment of α and γ-motoneurons in rats, dogs and humans

G. Schalow and B. Wattig [1]

Abstract

1. *Single fibre action potentials were recorded with 2 pairs of wire electrodes from human and dog lower sacral nerve roots and the rat nervus suralis. From the widths of single peaks of α_1 (FF), α_2 (FR), α_3 (S) (extrafusal) and γ_1 and γ_{21}-motoneurons (intrafusal) conduction velocity frequency distribution histograms were constructed and the limits of the velocity ranges determined. Distribution changes of conduction velocities in each group of α and γ-motoneurons were used for recruitment analysis in the occasional firing mode.*
2. *In the dog, the rat and the human, the slower conducting fibres were recruited before the faster conducting ones in each group of motoneurons. In the dog, the slowly conducting γ_1 and α_2-motoneurons were recruited directly following bladder catheter pulling, and the slowly conducting α_3-motoneurons were recruited 1 sec later. In the rat, the slowly conducting α_1-motoneurons were recruited directly following pin-pricking of the hindlimb, the slowly conducting α_2-motoneurons 0.2 sec later, and the slowly conducting α_3-motoneurons 1 sec later. In humans, the slowly conducting γ_1 and α_2-motoneurons were recruited 2 sec following bladder catheter pulling, the slowly conducting α_3-motoneurons 4 sec following pulling.*
3. *In the dog, with no additional stimulation slowly (and fast) conducting γ_{21} and α_3-motoneurons showed repeated activation 3 to 4 sec later. A subgroup of the α_1-motoneurons showed repeated activation every 2 sec. In the rat, without stimulation, a slower conducting subgroup of the α_1-motoreurons showed preferential activation of the low and high conduction velocities every 2 sec. In the human, with no additional stimulation, the slowly and fast conducting α_2 and α_3-motoneurons were recruited repeatedly every 2 sec.*

Key-words: Human — Sacral medulla — Recruitment — Occasional firing mode — Size principle — Repeated recruitment.

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 and defecation (9, 10, 13) in paraplegia. The concept includes a nerve anastmosis from the intercostal nerves rostral to the level of lesion to the lower sacral nerve roots, which originate in the caudal spinal cord. The research activities follow two lines. The practical aspect is concerned with the 'wiring' of mainly the peripheral nervous system of interest and with how 'rewiring' has to be performed. The reconnection of nerves requires detailed knowledge of the anatomy and the nerve fibre group composition of different nerves, the mismatch between reconnected nerves, and how the nerve roots can be identified during surgery both anatomically (9) and

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functionally (12). The theoretical line, the present work is aimed at contributing to, tries to clarify functions of the peripheral (PNS) and central nervous system (CNS) which are to be restored, namely the control of the urinary bladder and the rectum in normal and pathologic conditions. This kind of basic research is unavoidable, since connection with respect to function is only possible based on the understanding of functions of the human nervous system and of what has remained of them following spinal cord injury. Of special interest are interneurons, since they form the basis of plasticity which is needed for the relearning of functions.

The method of single-fibre action potential recording from whole nerve roots in humans was used to develop a precise classification scheme of nerve fibre groups in the PNS: the individual nerve fibre groups are identified by their group nerve fibre diameter and their group conduction velocity (11, 12, 14). Based on this classification scheme, receptor properties of skin, urinary bladder and anal canal have partly been analysed (12). Patterns of motoneuron impulsation generated in the human lower sacral spinal cord in response to natural stimulation have been characterised by the occasional firing mode, the transient and the continuous oscillatory firing mode (13). The recruitment of motoneurons in the occasional and oscillatory firing mode which drive anal and urinary bladder sphincters, will be analysed in a series of 6 papers. The first paper will report the physiologic recruitment of motoneurons and the second one the recruitment following spinal cord lesion, in the occasional firing mode. In the third paper the oscillatory firing will be analysed. The fourth paper will deal with impulse patterns of muscle spindle afferents, driving the oscillators, down to single pacemaker sites. In the fifth paper, the impulse patterns of the oscillators and the muscle spindle afferents will be directly compared, and in the sixth paper impulse patterns of intrafusal motoneurons will be compared with those of the spindle afferents and spinal oscillators. Clinical considerations will include possible biological treatments in spinal cord lesions.

The aim of this first paper is to further clarify the recruitment of motoneurons in the occasional firing mode (1, 2, 4, 6, 7). Henneman (1) showed that motor units in the gastrocnemius nerve were recruited according to their axonal conduction velocity (size principle) rather than by their type. Fleshman et al. (4) supported a higher structured recruitment scheme in which motoneurons are recruited according to type and conduction velocity in each group. In a previous work (15), γ_1, α_2 (FR) and α_3-motoneurons (S) were found to be recruited according to the size principle in each group: the slowly conducting α_2-motoneurons were recruited first, followed by α_3-motoneurons. The present paper will focus on the recruitment of α_1-motoneurons. It will be shown that α_1-motoneurons are recruited first, followed by α_2 and then α_3-motoneurons. Recruitment of motoneurons will also be analysed in a situation, where there is little or no stimulation at all.

Materials and methods

The methods used were described in previous publications (11, 12, 14). Data were obtained from measurements in a dog (Alsatian), a rat (Wistar, 110 days old), and 2 brain-dead humans (Hirntote = HTs) HT3 and HT6. The dog was anesthetised with Ketamine i.m. ($+(N_2+O_2)$), the rat was anesthetised with ether, and the blood pressure in the HTs was kept by administration of Dopamine (4 µg/kg per min), as in kidney removals.

Ethics

The measurements were done in accordance with the Helsinki Declaration, and were performed to reconstruct urinary tract functions as in kidney removals. The measurements in HTs, serving the development of a surgical technique in paraplegia, were approved by the Ethical Committee of then the GDR. As soon as the Committee has decided that the patient is brain-dead, the subject is considered a cadaver and no more a patient. Mostly cadavers are

transferred to urology department for kidney explantation or, after switching off the respirator, transferred to the pathology department for autopsy. Animal experiments are necessary for basic clinical research. However certain knowledge cannot be obtained from animals and why kill animals if in some cases more relevant knowledge can be obtained from human cadavers? In Germany (80,000,000 inhabitants) the number of paraplegics increase by approx. 1,300 yearly. About 130 of them commit suiside because of the 'no hope' situation. Others die because of pressure and infections in the urinary bladder, and the remainder live although the quality of their lives is low.

Electrophysiology

Single-fibre action potentials (APs) from nerve roots (Fig. 1A) and nerves (Fig. 3) were recorded extracellularly with 2 platinum wire electrode pairs (electrode pair distance = 8 mm; electrode distance in each pair = 4 mm) at 2 sites, pre-amplified (× 1000), filtered (RC-filter, passing frequency range 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 (JVC-Kasettenrecorder, Modell Nr. Hr-D250EG). A sharp 50 Hz filter was sometimes used between the pre-amplifier and the oscilloscope or, when playing back from tape, between the processor and the oscilloscope. Trace 'a' was the recording from the proximal pair and trace 'b' from the distal pair of electrodes. Conduction velocities of single axons were calculated from the conduction distance (electrode pair distance) and the conduction times. Conduction velocity frequency distribution histograms were constructed. Histogram classes were ≤ and <.

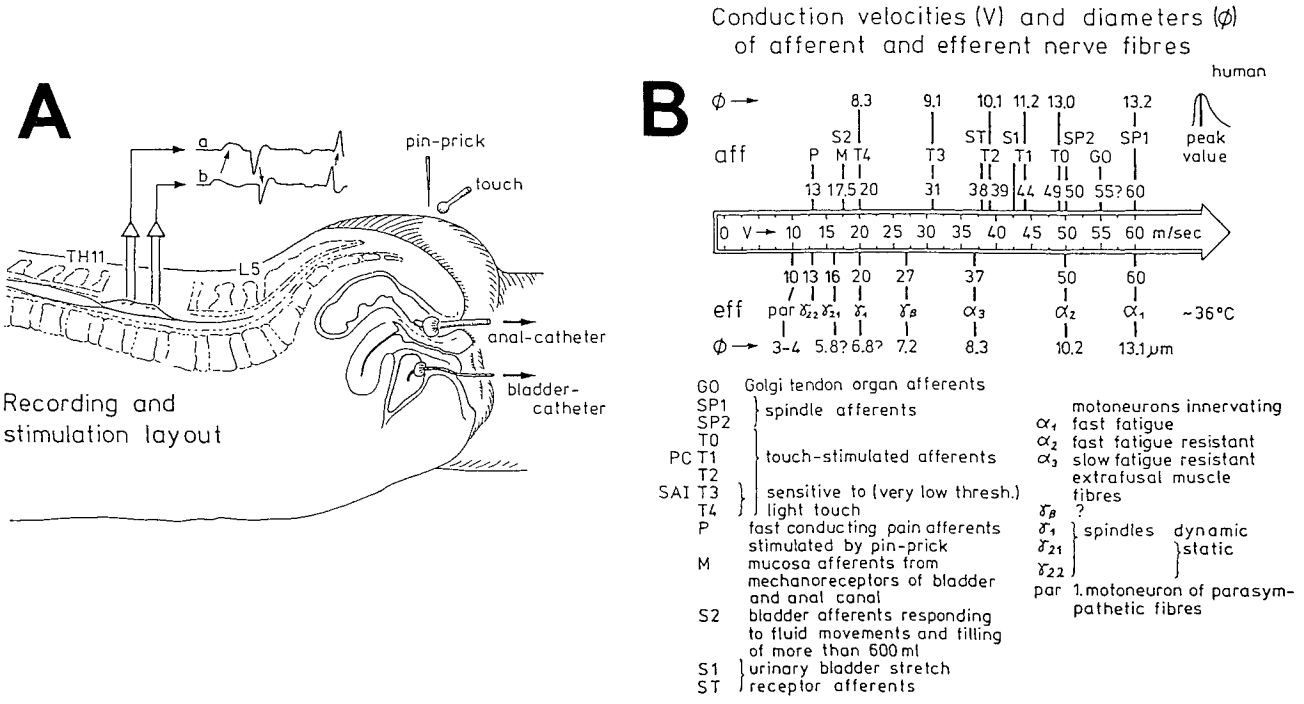

Fig. 1. — A. Layout for stimulation and recording of single-fibre action potentials (APs). Traces a and b are records from the 2 sites; downward arrow = efferent, upward arrow = afferent, the stimulations used were touch, pin-prick, anal and bladder catheter pulling.
B. Approximate peak values of group conduction velocities (V) (root temperature 36 °C) and group nerve fibre diameters (∅) of afferent and efferent nerve fibres in the cauda equina; human aged about 30 years. S1, ST, S2, M, P = afferents, with unknown corresponding nerve fibre diameters. M, S2 = possibly the same afferents. Insert: schematic representation of the frequency distribution shape of conduction velocities and nerve fibre diameters, peak value indicated.

Practical aspects of single-fibre AP recording are discussed in Ref. 14.

Morphometry

Root or nerve pieces of a few centimeters were removed after recording, fixated for 2 to 4 hours in 4% glutaraldehyde in cacodylate buffer, after-fixated in 1% OsO_4 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 ($\times 1000$). Nerve fibre diameters $\varnothing = 1/2\ (\varnothing_1 + \varnothing_2)$ ($\varnothing_1$ and $\varnothing_2$ are the larger and the smaller diameter of non-round-shaped fibres respectively) and the mean myelin sheath thickness, d, were measured by hand. The values were corrected for shrinkage (8%). The diameter values, measured for the nerve fibres were grouped into 4 ranges of myelin sheath thickness ($0.25 \leq d < 0.8$; $0.8 \leq d < 1.3$; $1.3 \leq d < 1.8$; $1.8\ \mu m \leq d < 2.3\ \mu m$).

Classification scheme for the human peripheral nervous system

Figure 1B summarizes the so far identified peak values of group conduction velocities and group nerve fibre diameters of nerve roots aprox. 3 cm distal to the sacral spinal cord. The group conduction velocities of static γ-motoneurons and parasympathetic fibres, as reported in paper VI (16), are included. This classification scheme is the basis for this and the following papers. Conduction velocities and nerve fibre diameters from measurements on dogs and rats have been adjusted to the classification scheme for humans.

Results

To analyse recruitment of extrafusal and intrafusal motoneurons in the occasional firing mode with the single-fibre action potential recording method, distribution histograms of representative conduction velocity frequencies have to be constructed from many, statistically distributed, recordings. The frequencies of the occurrence of first low and high velocities in a certain group of velocity distributions from single sweeps will then show recruitment changes, provided that the motoneurons in a group are activated with or with about the same frequency.

Distributions of representative conduction velocity frequencies of motoneurons

Dog

Single-fibre action potentials (APs) were recorded (see Fig. 1A) from a lower sacral root of a dog. Sweep pieces with APs of extrafusal (α) and intrafusal (γ) motoneurons are shown in figure 7B. The conduction times (ct) were measured and the corresponding conduction velocities (v) calculated (Fig. 7B). With the corresponding velocities from many sweeps, the representative frequency distribution histogram (Fig. 2A) was constructed. The limits of the different motoneuron classes were identified according to the distribution form of the motoneurons (shown in the inset of Fig. 1B); they are indicated in figure 2A. The fused peaks of the γ_1 and γ_{21}-motoneurons could be separated earlier (14, 15), and they were identified through the different functional properties of the γ_1 and γ_{21}-motoneurons. The columns for α_2, α_3 and γ_1-motoneurons in the histogram in figure 2A were filled, dotted and cross-hatched, to show more clearly the recruitment changes in the different groups.

Human

The distribution histogram of representative conduction velocity frequencies of the human dorsal S4 root motoneurons was constructed in the same way as above and is shown in figure 2B. The separation of γ_1 and γ_{21}-motoneurons is less accurate than in the previous case.

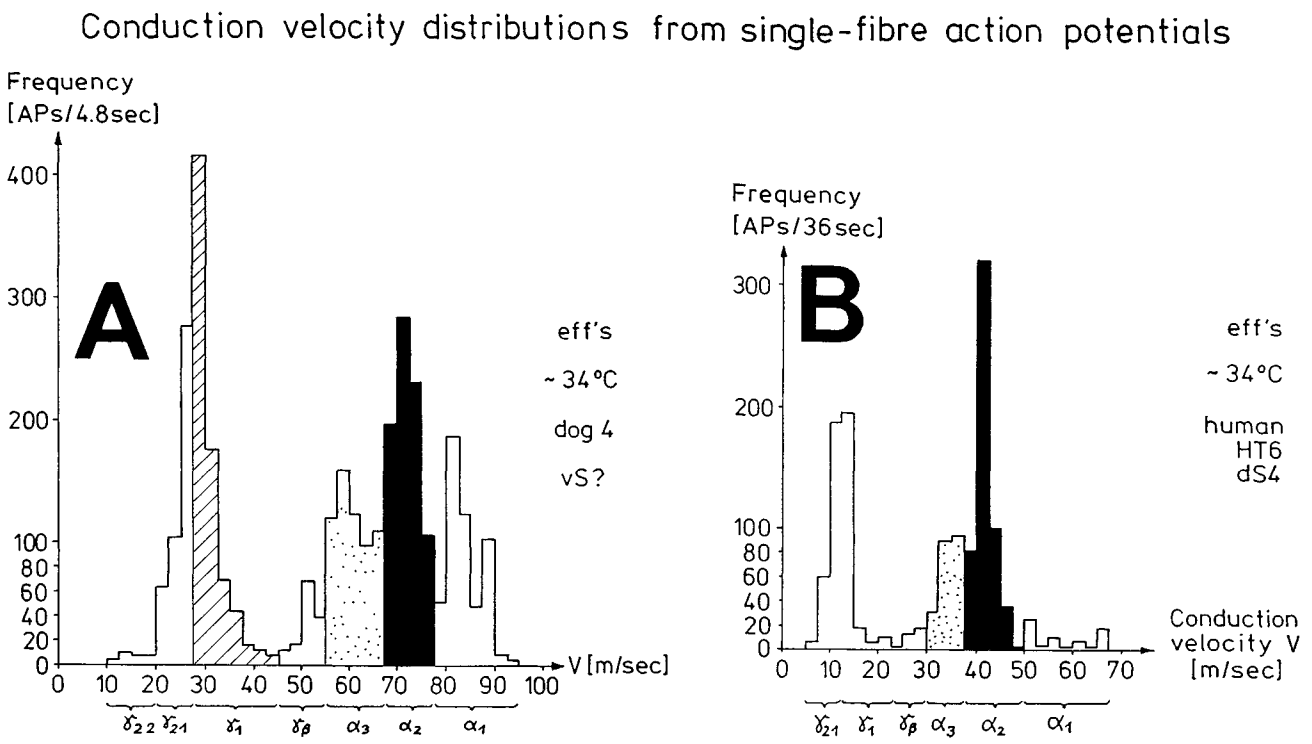

Fig. 2. — Distribution histograms of conduction velocity frequencies: efferent APs from dog (A) and human (B) lower sacral nerve roots. The distribution peaks are labelled according to the respective groups they represent. Motoneuron velocity ranges are indicated. In A, 24 sweeps of 0.2 sec, and in B, 30 sweeps (stimulated and non-stimulated) of 1.2 sec duration were used.

The group of γ-motoneurons will be analysed in more detail in paper VI (16). Original recordings of this root motoneuron APs were presented in an earlier paper (12) and will be treated in papers to follow.

Rat

Since there are no or only a few α_1-motoneurons in the lower human sacral roots, and as will be shown below, α_1-motoneurons in the comparable roots of the dog are only little activated with anal and bladder catheter pulling (no pronounced escape reaction), activation changes of rat α_1-motoneurons innervating hindlimb muscles will be added here to show the recruitment of α_1-motoneurons in relation to the recruitment of α_2 and α_3-motoneurons.

The rat nervus suralis is long enough to allow recording of single-fibre APs with the same set of recording electrodes as was used for the measurements in man and dogs. The rat nervus suralis contains also motoneurons which innervate foot muscles. Pin-pricking of the foot under a light ether anesthesia will activate the escape reaction of the rat, and α_1-motoneurons can thus be expected to be strongly activated. However peripheral nerves outside the spinal canal have an epineurium envelope. The epineurium soaked with saline solution will shunt extracellular APs and should therefore be removed. Since this is not completely possible, peripheral nerve recordings will not achieve the quality of the nerve root recordings. In addition, the rat nervus suralis shows variable fasciculation, which makes the dissection more complicated if one tries to choose a single fascicle. But as will be shown below, the recording quality from the rat nervus suralis was still sufficient to yield reasonably good distribution histograms of conduction velocity frequencies for afferents and efferents to calibrate the motoneuron velocity distributions and to

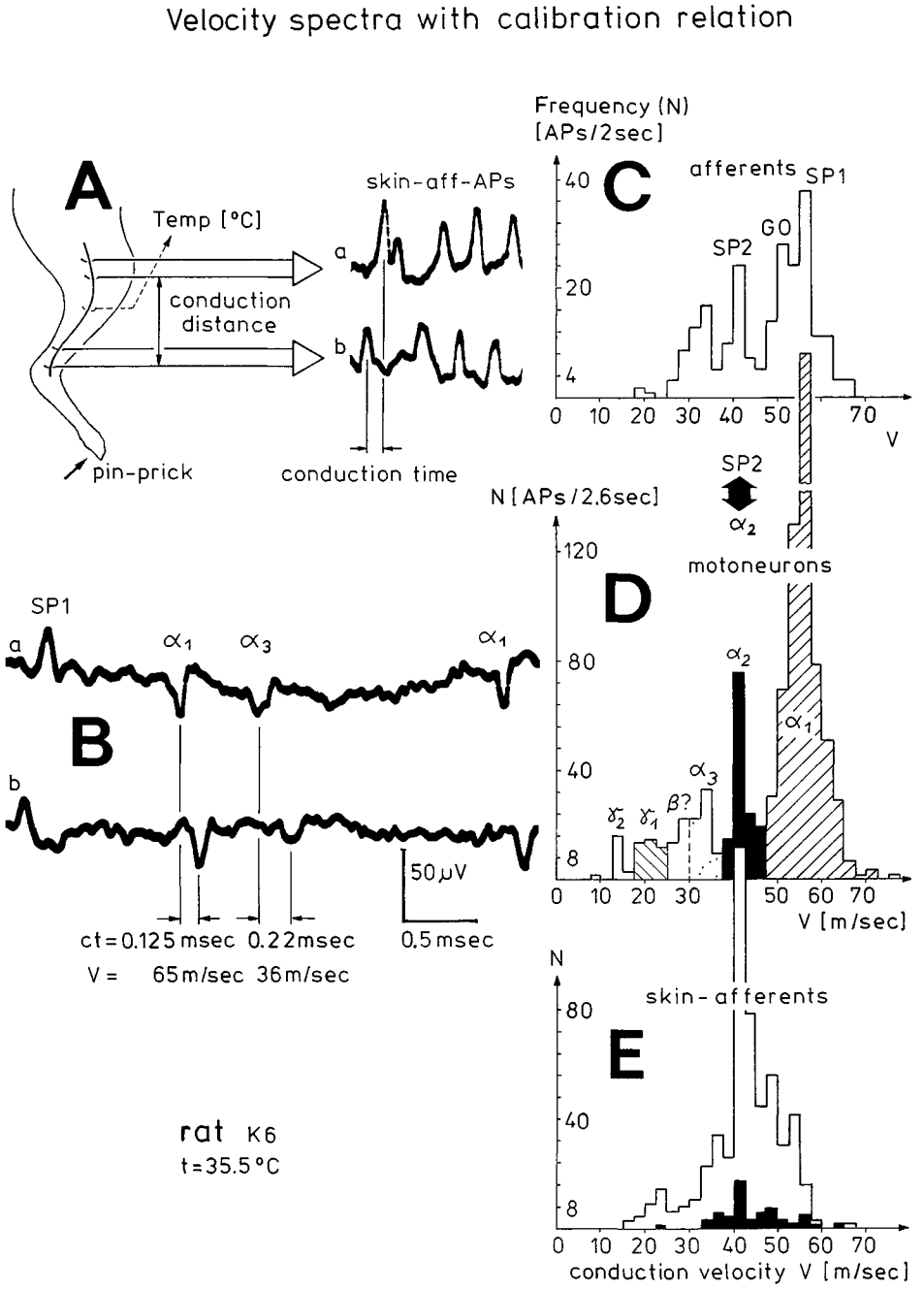

Fig. 3. — Recording of single-fibre action potentials (APs) from the rat nervus suralis, which contains also muscle nerve fibres (nervus plantaris lateralis). A. Stimulation and recording layout. B. Sweep piece of rat K6, 110 days old; conduction times (ct) and conduction velocities (v) are indicated. C, D, E: Distribution histograms of conduction velocity frequencies for muscle nerve afferents (C), extra- and intrafusal motoneurons (D), and skin afferents (E). Identified distribution peaks are labelled according to the respective group they represent (C, D). Note that α_2-motoneurons and secondary spindle afferents (SP2) conduct at the same velocity (calibration relation). Velocity ranges of α_3, α_2 and α_1-motoneurons are represented by dotted, filled or cross-hatched columns. In D, APs from 13 sweeps of 0.2 sec duration are summarized. The frequency ratios of AP occurrence with pin-prick: $\alpha_1 : \alpha_2 : \alpha_3 = 637 : 133 : 65 \approx 10 : 2 : 1$. E, the added velocities of skin afferents from 12 rats, each stimulated 2 times (the open column). The velocity histogram for rat K6 following one pin-prick is represented by the filled columns.

identify the different motoneuron groups with their velocity ranges in the representative velocity histogram; measurement of recruitment changes in α_1, α_2 and α_3-motoneuron classes is thus possible.

The layout for the recording from the rat nervus suralis is shown in figure 3A. The temperature of the nervus suralis was directly measured with a thermoelement and kept constant by heating with infra-red light. An original recording from rat K6 afferents and efferents is shown in figure 3B. Two conduction times (ct) and conduction velocities (v) are indicated. In figure 3B the motoneuron classes of origin of the APs were identified based on the velocity ranges of the individual motoneuron classes (Figs. 3C, D) and the respective conduction velocities. Figure 3C shows the conduction velocity distribution histogram for the afferents with no stimulation, and figure 3D shows the representative conduction velocity frequency distribution histogram for the motoneurons. In accordance with earlier measurements in humans (12), the nerve fibre classes, the peaks most likely belong to, were identified. The calibration relation of the conduction velocity frequency distribution histograms, namely that the secondary muscle spindle afferents conduct at about the same velocity as α_2-motoneurons (12), seems to hold also for the rat nervus suralis (Fig. 3D). The limits of the velocity ranges for the different motoneuron classes were drawn into figure 3D. Only the velocity ranges of α_1 and α_2-motoneurons are safe. Since the large α_1-motoneuron peak does not show the typical distribution form very well (Fig. 1B, inset) it might be that the rat α_1-motoneurons split into different subgroups similarly as α_1-motoneurons in the dog (14). By comparing figure 3D with figure 2 it is obvious that the rat α_1-motoneurons were much more activated than those of the dog.

The distribution histograms of conduction velocity frequencies for afferents activated by skin stimulation (light pin-prick) are shown in figure 3E. The filled columns refer to rat K6 and were obtained with 1 pin-prick. The open columns refer to 12 comparable rats and 2 pin-pricks each. It can be seen from figure 3E that a single stimulation in rat K6 already yielded the typical velocity distribution. By comparing figure 3E with figure 3D it can be seen that the largest skin-afferent velocity peak falls together with the α_2-motoneuron peak. This is different from the distributions obtained from man. There, the skin-afferents in the largest peak (probably innervating Pacinian corpuscles) conducted about 10% slowlier than α_2-motoneurons (12). Therefore, the afferents innervating the hairless skin of the rat hindlimb are probably not directly comparable to those innervating the hairless skin in humans or the peripheral and the central branch of the afferent cell are conducting with different velocities. Also the α_2-motoneuron may have a reduced diameter in the periphery.

Morphometry

Single-fibre action potential recordings from whole nerves or roots give detailed information about the afferent and efferent impulse traffic of the activated nerve fibres; but they provide no information about fibres which are not activated. A morphometric analysis of the nerve fibre diameters or similar values of the nerve cross-section provide information about all fibres, even though sometimes only little information can be extracted from it. Nevertheless it exactly says what nerve fibre population was recorded from.

The nerve fibre diameter spectra of the dog sacral root were discussed in Ref. 14; those of the human dorsal root were analysed in Ref. 12. The nerve fibre diameter spectra with respect to different myelin sheath thicknesses of the rat K6 nervus suralis are shown in figure 4. A representative part of the cross-section is shown in figure 4A. The corresponding fibre diameter distribution histograms are shown in figure 4B. Most likely the marked peak in the class of thick myelin sheaths contains primary spindle afferents (SP1) and α_1-motoneurons. No further peaks could be identified. This was to be expected, since besides skin afferents the rat nervus suralis contains also nerve fibres (afferents plus efferents) to foot muscle fibres,

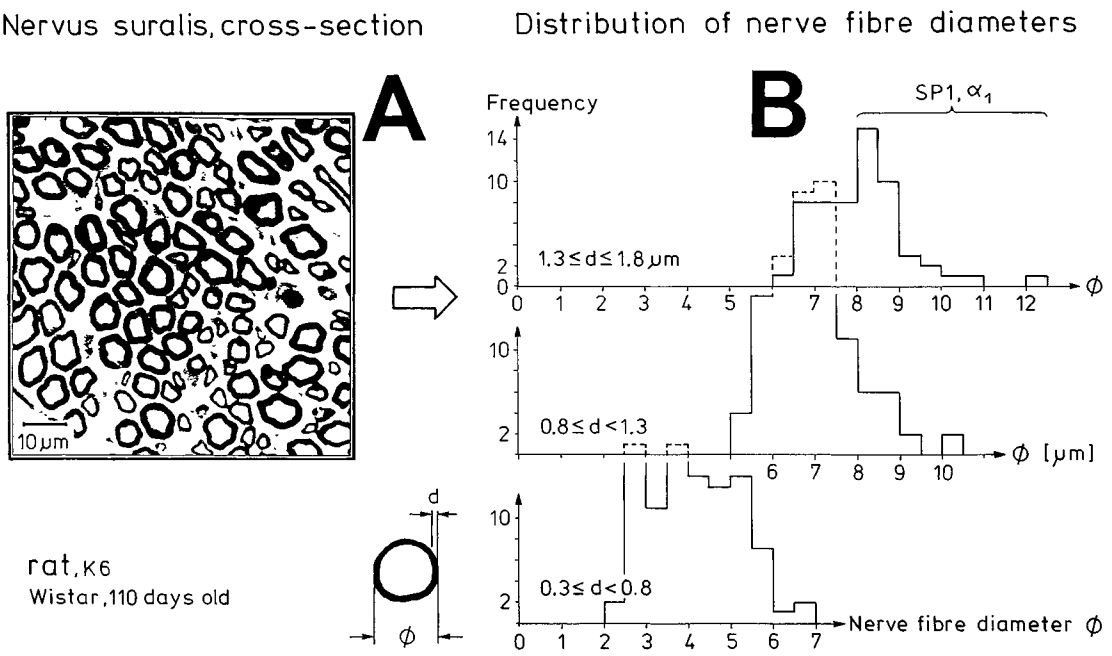

Fig. 4. — A. Portion of the cross-section of the nervus suralis measured electro-physiologically (Fig. 3). Thionin acridine-orange staining, contrasted with a copying-machine. B. Distribution histograms of nerve fibre diameter frequencies from the light microscope cross-section, partly shown in A. The ranges of the myelin sheath thicknesses, d, of fibres are given at each column. The distribution peak of primary spindle afferents (SP1) and α_1-motoneurons is indicated.

so that the distribution histograms of nerve fibre diameter frequencies will consist of too many nerve fibre groups to allow the identification of single group peaks, with the exception of groups with the thickest fibres.

Taking 8.5 µm as the peak value of the group diameters for α_1-motoneurons and primary muscle spindle afferents (SP1) (Fig. 4B) and using 56 m/sec as the peak value of the group conduction velocity for α_1-motoneurons and SP1-fibres (Fig. 3), a value of 6.6 is obtained for the ratio of conduction velocity and fibre diameter for α_1-motoneurons and SP1-fibres.

Recruitment in response to stimulation

Dog

Figure 5 shows distribution histograms of conduction velocity frequencies for motoneurons in a sacral root; they were constructed from single sweeps of 0.2 sec duration before and 0, 1, 2, 3 and 4 sec following stimulation. Since the frequencies of the occurrence of low and high velocities (marked with arrows) change in each motoneuron group, these frequency changes are interpreted as recruitment changes of activated motoneurons. This interpretation is based on the assumption that during the sweep all motoneurons fire only once or at least with roughly the same number of APs. This assumption is probably valid if all motoneurons fire in the occasional firing mode, since the next increase of conduction velocities follows at 4 sec (Fig. 5). However, α_2 and α_3-motoneurons can change their firing mode to oscillatory firing if high activity is needed. Continuously firing motoneurons can distort the corresponding velocity pattern in a group by raising the activity level. Transient oscillatory firing motoneurons may change the frequency distribution in their own group. But as long as clear recruitment changes occur repeatedly, the recruitment changes are real, even though oscillatory firing motoneurons may escape detection.

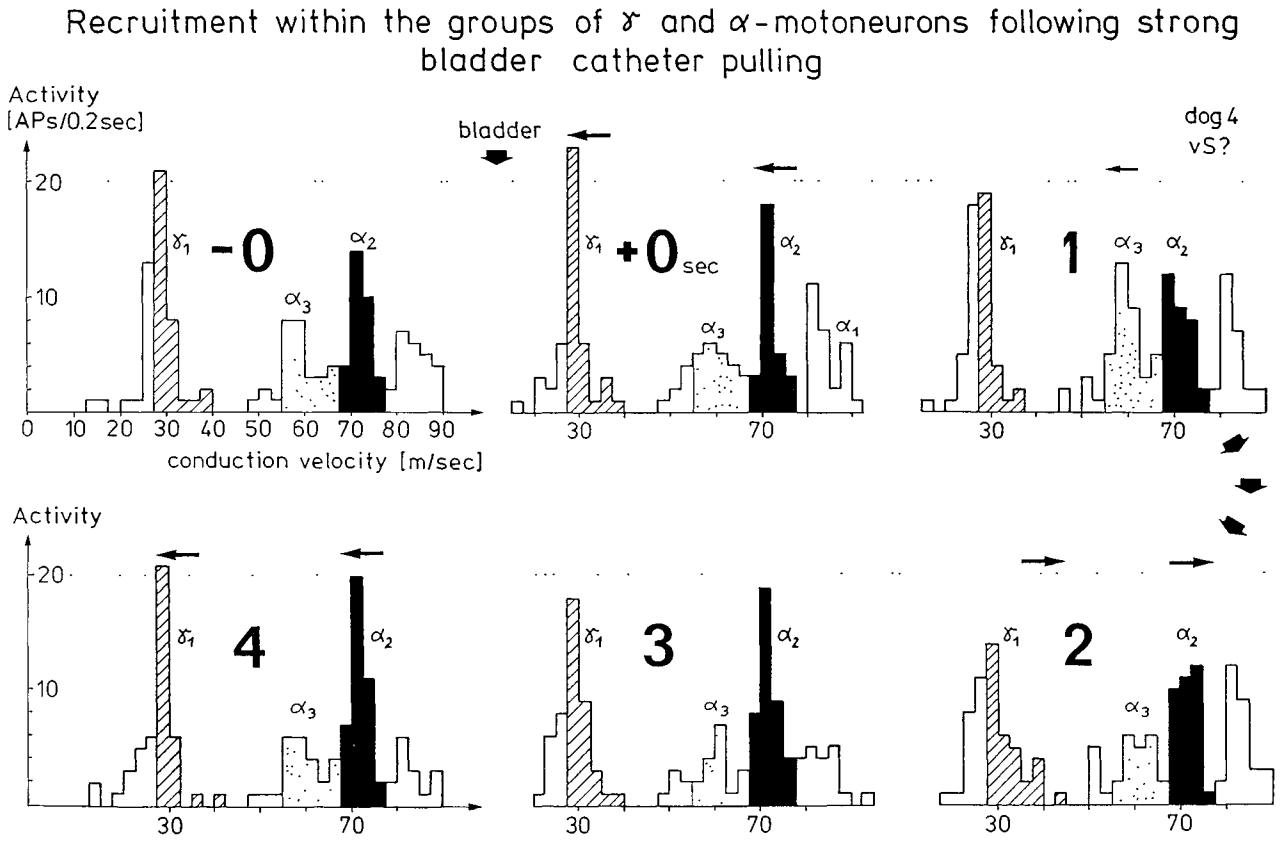

Fig. 5. — Frequency changes of single-fibre conduction velocities within the groups of γ_1, α_3 and α_2-motoneurons (recruitment) in a dog sacral root following strong bladder catheter pulling. The group conduction velocity ranges are taken from figure 2A. Time in seconds following stimulation is indicated (e.g. 1 sec: 1.0 to 1.2 sec); -0 and $+0$, 0.2 sec before and after the start of the stimulation. The arrow directions on top of the histograms indicate stages, in which motoneurons in a certain group with low or high velocities are preferentially activated, as can be calculated from the histograms. Columns for γ_1 are cross-hatched, those for α_3 are dotted, and those for α_2 are filled. Note that α_2-motoneurons are recruited before α_3-motoneurons, and the co-recruitment of γ_1 and α_2-motoneurons.

Following strong bladder catheter pulling (Fig. 5), slowly conducting γ_1 and α_2-motoneurons were preferentially co-recruited following stimulation and again 4 sec following stimulation. The fast conducting γ_1 and α_2-motoneurons were recruited preferentially 2 sec following stimulation. The slowly conducting α_3-motoneurons were recruited later than the slowly conducting γ_1 and α_2-motoneurons, namely 1 sec following catheter pulling. Other recruitment measurements of this case were presented in Ref. 15. It was shown there that γ_1 and α_2-motoneurons are only sometimes co-recruited. No clear recruitment can be seen for α_1-motoneurons. Probably, α_1-motoneurons were not strongly activated upon strong bladder catheter pulling, so that the summed activity from several motoneuron pools showed no clear-cut recruitment changes.

Rat

Figure 6A shows that α_1-motoneurons in the nervus suralis were recruited during the escape reaction, when the sole of the hindlimb was pin-pricked. It can be seen that the slowly conducting α_1-motoneurons were recruited directly following stimulation ($+0$), followed by α_2-motoneurons (0.2 sec) and α_3-motoneurons (1 sec). This measurement in the rat extends the recruitment order with respect to the different motoneuron groups to α_1-motoneurons; the slowly conducting α_1-motoneu-

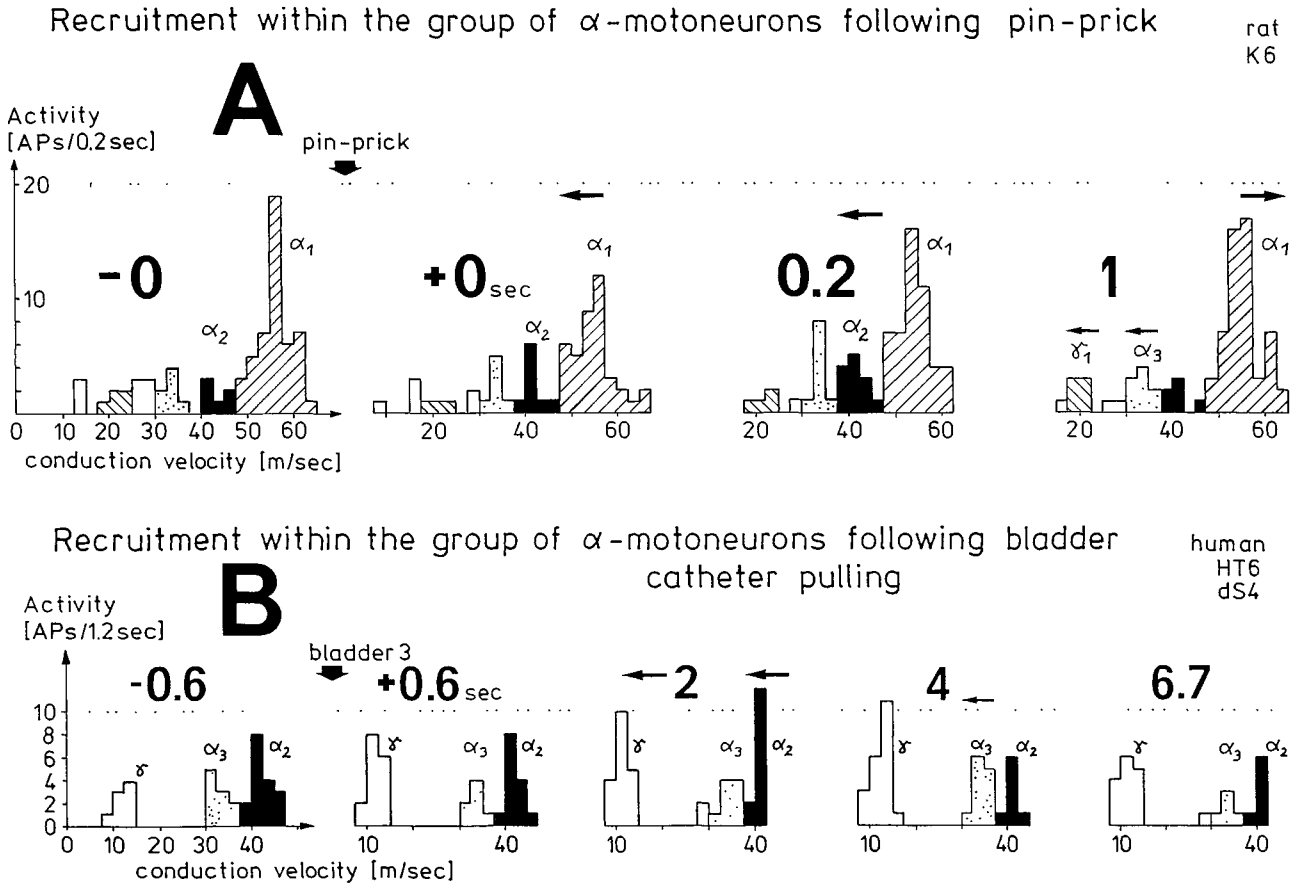

Fig. 6. — A. Frequency changes of single-fibre conduction velocities within the groups of α_2 and α_1-motoneurons in the rat nervus suralis following pin-prick. The velocity ranges are taken from figure 3D. +0 indicates interval of 0.2 sec following pin-prick. Note that α_1-motoneurons are recruited before α_2-motoneurons. B. Frequency changes of single-fibre conduction velocities within the groups of α_2 and γ_1-motoneurons in a human (HT6) sacral nerve root following strong bladder catheter pulling. The group conduction velocity ranges are taken from figure 2B. −0.6, +0.6, 2.4 and 6.7 are the times (half time of the 1.2 sec interval) in seconds before are after stimulation. Note the co-recruitment of γ_1 and α_2-motoneurons, and that α_2-motoneurons are recruited before α_3-motoneurons.

rons are activated first, followed by the slowly conducting α_2-motoneurons and then the slowly conducting α_3-motoneurons. The identification of the recruitment of γ_1-motoneurons is not safe. It seems as if they were not co-recruited with α_2-motoneurons.

Human

Figure 6B shows that in man the slowly conducting α_2-motoneurons were recruited (2 sec) before the slowly conducting α_3-motoneurons (4 sec). Maybe, γ_1-motoneurons were in this case co-recruited with α_2-motoneurons. For further data see Ref. 15.

As suggested by the measurements in the dog and by earlier results (15), the motoneurons in each group are re-recruited rhythmically every 3 to 4 sec according to the conduction velocity (size principle) if the duration of stimulation, i.e. the afferent activity increase, is sufficiently long. The question arises, how the recruitment of motoneurons is regulated if there is no additional afferent input. How is the firing of motoneurons for the so-called muscle tone when the afferent input is nonspecific and orginates in different parts of the body from different receptors. The problem is rather intricate, since the activity levels of the motoneurons are low, and there is no fixed starting

point for the recruitment analysis, so that often the analysed sweeps hit intermediate recruitment stages, if periodic recruitment exists at all.

Recruitment upon no additional stimulation

Dog

Figure 7A shows the recruitment of motoneurons upon no additional stimulation, apart from the positioned bladder catheter. Low and high conduction velocities in the γ_{21} and α_3-motoneuron groups show an increased frequency of occurrence at different times. Also, α_1-motoneurons seem to show rhythmic activation changes. The periodicity is about 3 to 4 sec for γ_{21} and α_3-motoneurons. The γ_{21} and α_3-systems seem to be activated independently of each other. The stages when there is highest activation of slowly or fast conducting motoneurons does not seem to fall together with the time periods of the sweeps chosen. The α_1-motoneurons seem to show repeated activation every 2 sec. Because the velocity changes are limited to rather low value ranges, these α_1-motoneurons seem to belong to the $\alpha_{11} = (\alpha_{Int})$-type.

Rat

In the measurement in the rat (Fig. 8A) α_1-motoneurons were recruited approx. every 2 sec. Again, a slowlier conducting subgroup seems to be activated repeatedly. Of special interest is here that this measurement was taken before the first pin-prick. Further, the depth of the ether anesthesia was not constant: it strongly weakened from 0 sec to 3.3 sec, as reflected in an overall activity increase. During

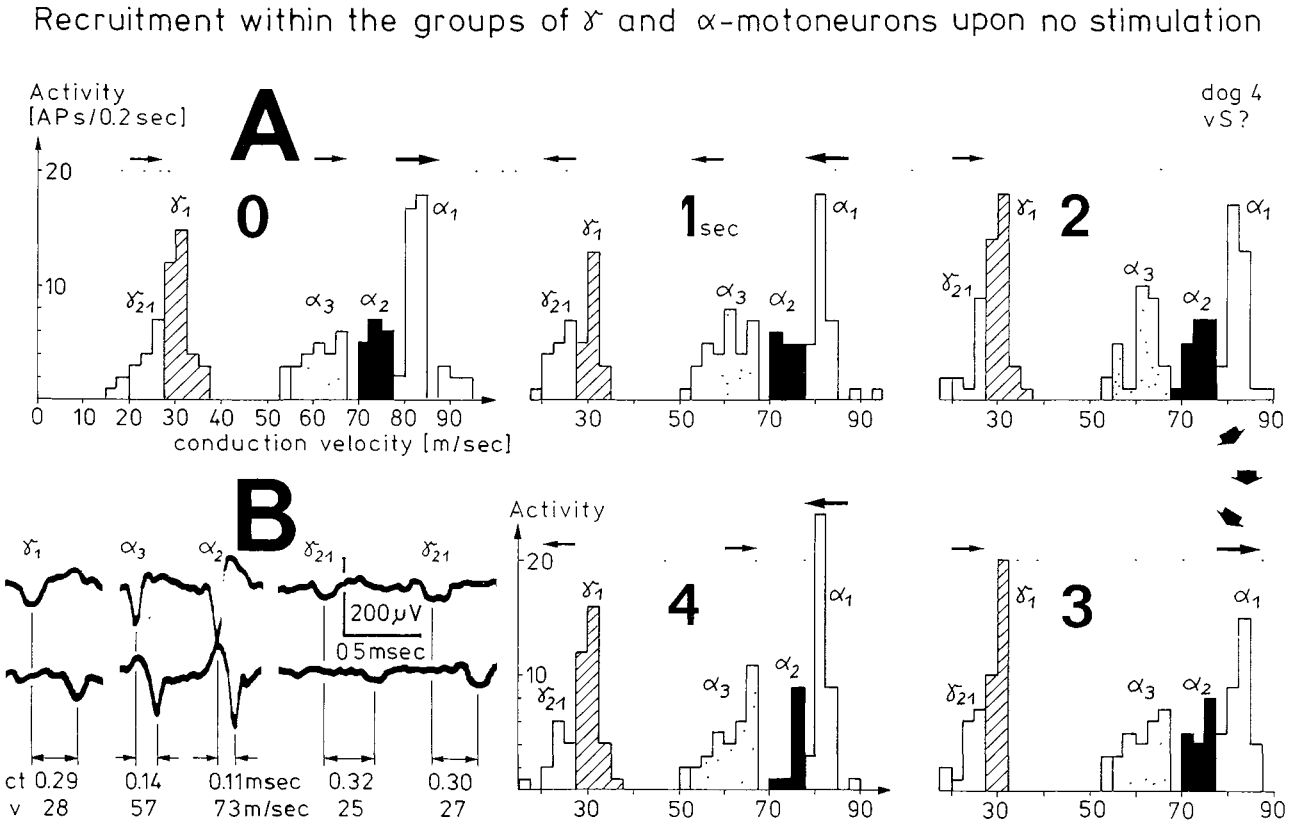

Fig. 7. — Frequency changes of single-fibre conduction velocities within the groups of α and γ-motoneurons upon no stimulation; dog, bladder catheter positioned. For symbols see legends to previous figures. B. Sweep piece from a recording of dog 4. Conduction times (ct) and conduction velocities (v) and α and γ-motoneurons are indicated.

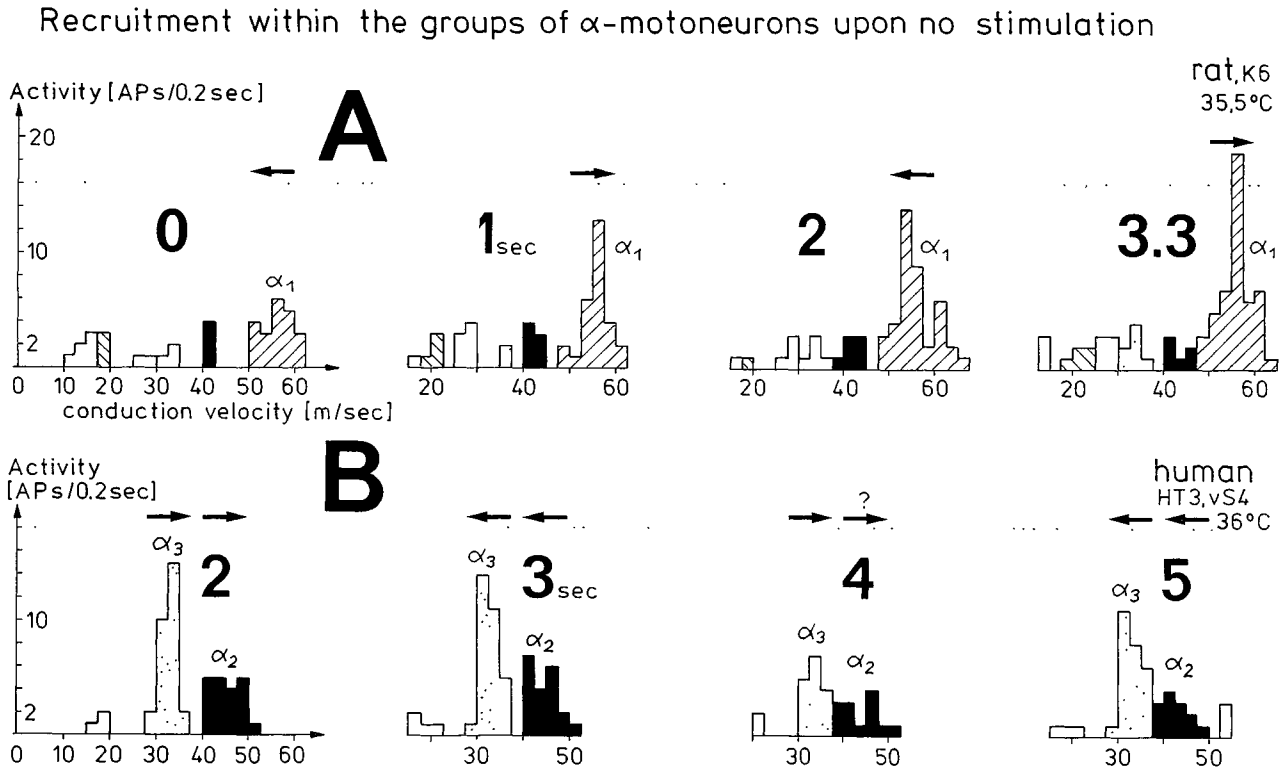

Fig. 8. — Recruitment changes of α and γ-motoneurons in the rat (A) and in man (B) (HT3) upon no stimulation (no catheter positioned). The velocity ranges in A are taken from figure 3D. The activity increase in A with time (from 0 sec to 3.3 sec) is due to the weakening of ether anesthesia. In B, no histogram is shown to enable identification of the velocity ranges; see Ref. 11. Other symbols as in previous figures.

deep ether anesthesia no or nearly no efferent activity was recorded following pin-prick. Therefore with the weakening of anesthesia (Fig. 8A) efferent activity appeared (upon no stimulation): α_1-motoneurons were recruited repeatedly, according to the size principle. Even though the rat was not stimulated (no catheter was positioned either), there probably was afferent input to the spinal cord from pain receptors from the wound area and with the weakening of anesthesia, this pain (and other) afferent input was processed in the CNS.

Human

Since the efferent activity of the dorsal S4 root of HT6 was too low in the non-stimulated case, recruitment with no stimulation was measured in an other HT (the ventral S4 root of HT3). The morphometry data were reported in Ref. 11. Figure 8B shows that α_2 and α_3-motoneurons are recruited rhythmically every 2 sec. The co-recruitment of α_2 and α_3-motoneurons is probably accidental. Since there was no catheter used with HT3, it is concluded that there are ongoing recruitment changes with no specific stimulation also in humans.

Discussion

It has been shown that single-fibre action potentials can also be recorded from the nervus suralis of the rat. Since the rat nervus suralis contains also nerve fibres to foot muscles, distribution histograms of conduction velocity frequencies can separately be constructed from skin afferents, motoneurons and non-skin afferents measured simultaneously. Also, the calibration relation of the velocity distributions is valid: α_2-motoneurons and secondary spindle

afferents conduct with the same velocity (12). Even though the single-fibre action potential recording from the peripheral nervus suralis provides less information than human root recordings (where no epineurium and nearly no perineurium in ensheathing the root) and in contrast to human ventral roots, the suralis morphometry supplies nearly no information about single peaks of nerve fibre groups, simultaneous analysis of single-fibre action potentials and nerve fibre diameters of the rat nervus suralis is a comparable powerful tool: it is sheap and easy to handle. With this animal model one can study e.g. regeneration, artificially induced diabetic neuropathies or effects of drug therapy (18).

By correlating the group conduction velocity for α_1-motoneurons of a 110 days old Wistar rat (Fig. 3) with the group nerve fibre diameter (Fig. 4), a conversion factor of 6.6 was calculated for conduction velocity to nerve fibre diameter. This value is roughly in accordance with classical measurements (5, 8). It has been shown in humans (12) and dogs (14) however, that the conversion factor of myelinated fibres is different for different nerve fibre groups (12). For α_1-motoneurons of 110 days old Wistar rat at about 36 °C the conversion factor was 6.6, while being 5.1 in an Alsatian dog (α_{12}-motoneurons) (14) and 4.6 (12) in man. Boyd et al. (19) found a mean ratio of 5.7 for the largest fibres and 4.5 for the slower ones in the cat. In the baboon the conduction velocity to fibre diameter ratio is about 5.2 for the fastest fibres (20).

It has been shown in this and a previous publication (15) that motoneurons were recruited in their group according to the size principle; this means that slowly conducting motoneurons in each group were activated before the faster conducting motoneurons. But as shown previously (see Ref. 15 and Fig. 5), the motoneurons are recruited again 3 to 4 sec later if the afferent input was sufficiently long. As shown in table 1 of Ref. 15, γ_1-motoneurons (intrafusal) were sometimes also repeatedly recruited every 2 sec.

Upon no (specific) stimulation α_3-motoneurons (Fig. 8B) showed repeated recruitment every 2 sec. It has to be clarified further what the time periods are for repeated recruitment and whether the repeated recruitment is different with and without stimulation. In a next paper dealing with recruitment in humans with spinal cord lesions the conditions for measurement of recruitment upon no stimulation will be better, since higher activity levels can be expected because of afferent sprouting to former tract synapses.

It can be seen from figures 7 and 8B (no specific stimulation) that α_3 and γ_{21}-motoneurons show more pronounced recruitment than α_2 and γ_1-motoneurons. This indicates that static extra and intrafusal motoneurons of the pelvic floor are activated quite strongly, associated with the weight carrying of the pelvic floor or similar structures in the dog.

It has been shown in this and a previous publication that the motoneurons in each group are recruited at certain times following stimulation. On the other hand, there is ongoing recruitment in the occasional firing mode with no specific stimulation. Therefore, with strong (specific?) stimulation the motoneurons in each group are activated according to the size principle. Mostly, new activation is not in phase with the ongoing one, but the recruitment followed the phase of new activation. If the spinal circuitries responsible for the periodic recruitment of the different motoneuron groups are the same for strong specific activation and low-level nonspecific activation, then with strong stimulation the recruitment phase is changed, and the amplitude of activation declines with time to the low level of the nonspecific afferent input. If there exists a separate circuitry responsible for the high activation and another one for the low level activation (in the occasional firing mode), then there will be a break when the recruitment changes from the high to the low level activation. This speculation may not be hypothetical, since if one very strongly activates α_2-motoneurons over a longer interval, they start to fire in the oscillatory mode with impulse trains at about every 160 msec (13). But when the specific afferent input is terminated, another circuitry arrangement takes over, which activates α_2-motoneurons in the

occasional firing mode at a periodicity of 2 to 4 sec. The silent period (3, 17) could also be a break between two different firing modes, driven by different spinal circuitries; one of them in this case is the monosynaptic reflex arc.

It remains unclear whether with the recruitment in the occasional firing mode all motoneurons of a certain motoneuron group are activated or not. Motoneurons can simultaneously belong to different motoneuron pools. Are both motoneuron pools recruited in phase? The unambiguous observation of repeated recruitment in the sacral root of the dog, where probably leg, tail and sphincter functions are contained, point towards the same recruitment phase. The circuitry in the CNS may serve several motoneuron pools with the same recruitment speed, according to different afferent inputs to the different motoneuron pools however, their activation patterns are quite different.

References

1. BAWA, B., BINDER, M.D., RUENZEL, P. and HENNEMAN, E.: Recruitment of motoneurons in stretch reflexes is highly correlated with their axonal conduction velocity, *J. Neurophysiol.*, 52: 410-420, 1984.
2. DESMEDT, J.E.: Size principle of motoneuron recruitment and the calibration of muscle force and speed in man. In: J.E. Desmedt (Ed.), *Motor Control Mechanisms in Health and Disease*, Raven Press, New York, pp. 227-251, 1983.
3. DIETRICHSON, P.: The silent period in spastic, rigid, and normal subjects during isotonic and isometric muscle contraction. *Acta Neurol. Scandinav.*, 47: 183-193, 1971.
4. FLESHMAN, J.W., MUNSON, J.B., SYPERT, G.W. and FRIEDMAN, W.A.: Rheobase, input resistance, and motor unit type in medial gastrocnemius motoneurons in the cat. *J. Neurophysiol.*, 46: 1326-1338, 1981.
5. GASSER, H.S. and GRUNDFEST, H.: Axon diameter in relation to the spike dimensions and the conduction velocity in mammalian A fibres. *Am J Physiol.*, 127: 393-414, 1939.
6. GUSTAFSSON, B. and PINTER, M.J.: Relations among passive electrical properties of lumbar α-motoneurones of the cat, *J. Physiol.*, 356: 401-431, 1984.
7. HERDMAN, J., REINERS, K. and FREUND, H.-J.: Motor unit recruitment order in neuropathic disease. *Electromyogr. Clin. Neurophysiol.*, 28: 53-60, 1988.
8. HUNT, C.C.: Relation of function to diameter in afferent fibres of muscle nerves, *J. gen. Physiol.*, 38: 117-131, 1954.
9. SCHALOW, G.: The problem of cauda equina nerve root identification. *Zbl. Neurochirurgie*, 46: 322-330 (1985).
10. SCHALOW, G., AHO, A. and LANG, G.: Nerve fibre counts for an intercostal to cauda equina nerve root anastomosis, *Zent. bl. Chir.*, 112: 457-461, 1987.
11. SCHALOW, G.: Efferent and afferent fibres in human sacral ventral nerve roots: basic research and clinical implications, *Electromyogr. Clin. Neurophysiol.*, 29: 33-53, 1989.
12. SCHALOW, G.: 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, 1991.
13. SCHALOW, G.: 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, 1991.
14. SCHALOW, G. and BARTH, H.: Group conduction velocities and nerve fibre diameters of α and γ-motoneurons from lower sacral nerve roots of the dog and humans, *Gen. Physiol. Biophys.*, 11: 85-99, 1992.
15. SCHALOW, G.: Recruitment within the groups of γ_1, α_2 and α_3-motoneurons in dogs and humans following bladder and anal catheter pulling, *Gen. Physiol. Biophys.*, 11: 101-121,1992.
16. SCHALOW, G.: Action potential patterns of intrafusal γ and parasympathetic motoneurons, secondary muscle spindle afferents and an oscillatory firing α_2-motoneuron, and the phase relations among them in humans, *Electromyogr. Clin. Neurophysiol.*, 33: 477-503, 1993.
17. MERTON, P.A.: The silent period in a muscle of the human hand. *J. Physiol.*, 114: 183-198, 1951.
18. WATTIG, B., SCHALOW, G., HEYDENREICH, F., WARZOK, R. and CERVOS-NAVARRO, J.: *Nucleotides enhance nerve fibre regeneration after peripheral nerve crush damage — Electrophysiologic and Morphometric investigation*, Drug Research, in press.
19. BOYD, I.A. and DAVEY, M.R.: *Composition of peripheral nerve*, pp. 1-57, Livingston, Edinburgh, 1968.
20. MCLEOD, J.G. and WRAY, S.R.: Conduction velocity and fibre diameter of the median and ulnar nerves of the baboon. *J. Neurol. Neurosurg. Psychiat.*, 30: 240-247, 1967.

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