Recruitment Within the Groups of γ_1, α_2 and α_3-Motoneurons in Dogs and Humans Following Bladder and Anal Catheter Pulling

G. SCHALOW

Department of Neuropathology, Klinikum Steglitz,
Freie Universität Berlin,
and Department of Neurosurgery,
Ernst-Moritz-Arndt Universität (Pommern-Universität),
Greifswald, Germany

Abstract. Conduction velocity frequency distribution histograms were constructed from lower sacral root recordings of single intrafusal (γ) and extrafusal (α) motoneurons. The velocity distributions of occasional and stimulated activity before and following bladder and anal catheter pulling were almost identical for dogs and humans. The limits of the velocity ranges of α_1(FF), α_2(FS) and α_3(S) and γ_β(?)-motoneurons were determined from the broadness of the single peaks. The borders of the partly fused peaks of γ_1 and γ_{21}-motoneurons were estimated from their different functional properties. Activity levels of the α_1, α_2, α_3, γ_β, γ_1 and γ_{21}-motoneurons were too complex to allow safe conclusions from the dog measurements, probably because of the representation of leg and tail in addition to sphincter functions in the lower sacral root. In the human dorsal S4 root, in which mainly efferent functions of sphincters only were contained, the γ_{21}, γ_1, α_2 and α_3-motoneurons showed simple behaviour.

Distribution changes of conduction velocities in each group of α and γ -motoneurons were used for recruitment analysis. Following stimulation in dogs and humans, within the groups of γ_1, α_3 and α_2 -motoneurons, slowly conducting fibres were activated before the faster conducting ones. The α_3 -motoneurons were recruited later than the α_2 -motoneurons.

In the dog, low γ_1 and α_2 -motoneuron velocities occurred preferentially 0 to 0.2 s following strong bladder catheter pulling, probably in the mono- and oligosynaptic pathways. Low conduction velocities of α_3-motoneurons occurred more often 1 to 1.2 s following stimulation. At 2 to 2.2 s following stimulation, the high γ_1 and α_2-motoneuron velocities were more activated. At 4 to 4.2 s following stimu-

Correspondence: Dr. Dr. Giselher Schalow, Weddigenweg 49,
D 1000 Berlin 45, Germany

lation, low γ_1 and α_2-motoneuron velocities were recruited again. Following strong bladder catheter pulling, co-recruitment of the γ_1 and α_2-motoneurons seemed to occur.

Following anal catheter pulling in the dog there was no co-recruitment of γ_1 and α_2-motoneurons. In the case of γ_1-α_2 co-recruitment, the γ_1-motoneurons were recruited additionally once in between the co-recruitment. The higher frequency of recruitment of the γ_1-motoneurons, and the separate recruitment of the γ_1 and α_2-systems, indicate that the activation of γ_1 and α_2-motoneurons are not strongly linked.

In humans, where there are no, or only few mono and disynaptic pathways with respect to sphincter activity, low conduction velocities of α_2-motoneurons increased only 1.4 to 2.6 s following strong bladder catheter pulling. Probably this recruitment originated in the polysynaptic pathways. The γ_1-motoneurons seemed to also be co-recruited with the α_2-motoneurons. The α_3-motoneurons seemed to be recruited only 3.6 to 4.6 s following stimulation.

In measurements on humans, the recruitment could roughly be correlated to the activity increase following stimulation. This was not, or only partly possible, in the measurements on dogs.

The co-operation and the separate activation of the γ_1 and α_2-motoneuron systems is discussed with respect to plasticity in spinal cord lesions.

Key words: Dogs — Humans — Intrafusal motoneurons — Extrafusal motoneurons — Recruitment

Introduction

Continence of the urinary bladder and the rectum is a precondition of normal life. Functions of the external sphincters are an important component, and their understanding is necessary for pathology repair.

Following pulling of bladder and anal catheters, exteroceptive and interoceptive afferent inputs (Schalow 1991a) enter the spinal cord and, according to the physiologic organization of the spinal cord certain pathways and responses are channeled to the central nervous system (CNS). The extra- and intrafusal motoneurons represent the final common path of all CNS motor commands. Some factors regulating motoneuron discharge, such as spinal circuitry (spinal oscillators (Langhorst et al. 1986, Schalow 1991b)), synaptic drive, susceptibility to discharge determined by the properties of the sensitive initial axon segment, and somatic membrane and activation history, have partly been analyzed earlier (Schalow 1991b, 1991c). The recruitment and discharge pattern that is produced in motoneurons by a particular combination of these factors determines the characteristics of the ensuing muscle contraction. In this work the recruitment order and recruitment speed of γ_1, α_2

and α_3-motoneurons were directly measured and compared with their discharge frequency level.

In the existing recording situation here, an increased recruitment following stimulation is paralleled by an increased discharge rate among already active motoneurons. In records obtained from dogs, sphincter motoneuron discharge is mixed with non-sphincteric motoneuron activity, mainly from motoneurons innervating tail muscles. Measurements in human root mainly reflected sphincteric motoneurons and functionally associated motoneurons innervating the pelvic floor muscles.

Two different opinions exist concerning the recruitment of motoneurons (Bawa et al. 1984, Desmedt 1983, Fleshman et al. 1981, Gustafsson and Pinter 1984, Herdman et al. 1988, Kanda and Desmedt 1983, Kernell 1983). According to one of them, the recruitment order follows mainly the motor-unit type (Fleshman et al. 1981). However, Hennemans' group (Bawa et al. 1984) showed that motor units in the gastrocnemius nerve were recruited according to their axonal conduction velocity (size principle) rather than by their type. The measurements of this work support a higher structured recruitment scheme (Fleshman et al. 1981) in which extra- and intrafusal motoneurons are recruited according to type and conduction velocity in each group, and where at least the recruitment speed also has to be taken into consideration. If in the "type - versus - size" controversy orderly recruitment depends also on motor unit type, reversals in recruitment order with respect to axonal conduction velocity should occur. In this paper it will be reported that α_3-motoneurons with lower conduction velocities were recruited later than α_2-motoneurons. The measured recruitment of the γ_1-motoneurons seems to be a new observation.

The nomenclature used is that α_3, α_2 and α_1-motoneurons innervate muscle fibres of the S, FR and FF type respectively (Burke et al. 1973, Desmedt 1983, Schalow 1991c).

Materials and Methods

As described previously (Schalow and Barth 1992), recordings were taken from the lower sacral nerve roots (S4 in the human case) using two pairs of wire electrodes. The recordings were also stored on a video tape. Conduction velocity frequency distribution histograms were constructed from the conduction times and the corresponding velocities of the single action potentials (APs) of dogs and a brain-dead human individual (HT). Discharge rates and velocity distribution changes (recruitment) in each group were analyzed. Since pressure, stretch, drying up of roots, ion fluid composition changes from washing and root wettening, and deficit in blood supply may deform the AP shape and reduce the conduction velocity, only the best recordings were used for a thorough analysis of conduction velocity distribution changes in each motoneuron group. Similar analyses must be based on high quality recordings to be able to identify all afferent and efferent APs (internal consistency); this is more important than to have a high number of measurements.

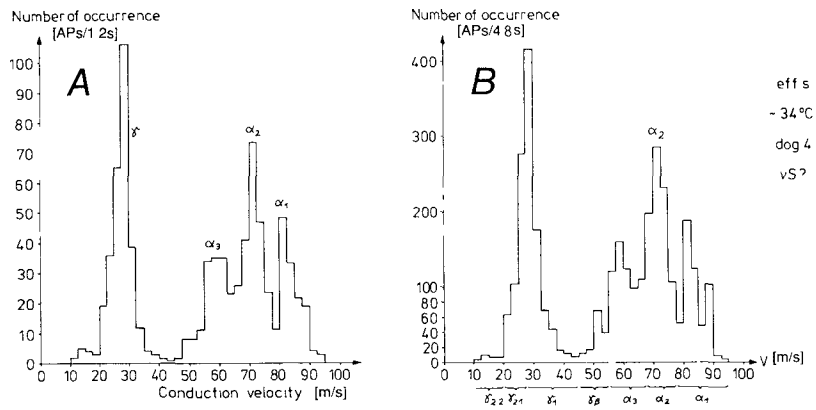

Figure 1. Distribution histograms of conduction velocity frequencies in a ventral sacral root. A: values from 6 sweeps of 0.2 s duration before and between stimulations. B: values from 24 sweeps of 0.2 s duration distributed over 20 s following bladder and anal catheter pulling. γ_{22}, γ_{21}, γ_1=intrafusal motoneurons; γ_β=?; α_3, α_2, α_1=extrafusal motoneurons. Velocity ranges of the motoneuron groups shown in B.

Apart from laminectomy, the recordings were taken from undamaged dog and HT nervous system.

Results

Conduction velocity distributions of occasional and stimulated efferent activities

Dog

Fig. 1 shows conduction velocity distribution histograms of intrafusal (γ) and extrafusal (α) motoneurons before and between stimulation (A), and during and following stimulation (B). Using a high number of measurements for the histogram of stimulated activity, Fig. 1 shows that the histograms of occasional and stimulated activity are almost exactly the same. It is therefore justified to establish velocity ranges of the different α and γ -motoneurons as shown in the lower part of Fig. 1*B*. The distribution of stimulated activity from single sweeps of 0.2 s duration can look very different, as can be seen from Figs. 5 and 6.

The establishing of the α-motoneuron classes is rather easy, because their single distributions are clearly distinguishable. The identification is loaded by an error of 10 to 20%, because of the overlapping of the neighbouring distributions. The establishment of the border between the γ_{21} and γ_1-motoneurons is more difficult since their distributions overlap. The shape of the whole γ-peak suggests that

this peak consists of 2 fused peaks, since the distribution does not have the form of a single nerve fibre group distribution (Schalow 1989, Fig. 5 in Schalow 1992). By setting different borders between the γ_{21} and γ_1-motoneurons and calculating activities it was found that the most likely border between the two γ-motoneuron groups is that given in Fig. 1B, as the static γ_{21}-motoneurons behave differently from the dynamic γ_1-motoneurons (Granit et al. 1957, Schalow 1991c). The error of the calculated activities due to the overlap of the distributions will be larger for the γ than for the α-motoneuron groups. The γ_{22}-motoneuron peak is very small, and will not be used later for the calculation of activity changes. Probably this peak is larger since many γ_{22}-action potentials (APs) were lost in the noise and artifact level, or their small amplitude was overlapped by APs of larger amplitude (Fig. 1 in Schalow 1992). It is possible that 1 or 2 α-motoneurons were in the oscillatory firing mode (Schalow 1991b) because of the constant stretch reflex caused by the anal catheter. Sometimes it seemed as if there was oscillatory firing (Schalow 1991b) present. The high activity level made it impossible to safely identify motoneurons in the oscillatory firing mode.

Human

The distribution of efferent conduction velocities of a human dorsal S4 root was shown in a previous paper (Schalow and Barth 1992, Fig. 5). This distribution of occasional and stimulated activities (no oscillatory firing contained) is, apart from the velocity values, similar to that obtained for dogs, even though the distribution forms of the different peaks are not as pronounced. The 30 sweeps of 1.2 s duration were sufficient for this correlation. A further increase would bring no more information since the number of motoneurons with a diameter larger than 5.5 μ m in the dorsal root was only 18 % (Schalow 1991a). The recordings and the morphometry of this dS4 root were analyzed previously (Schalow 1991a, b, c). However, the improved classification of γ -motoneurons (Schalow and Barth 1992), with the help of the data, obtained from the dog, allowed to calculate motoneuron activities of separately for γ_1 and γ_{21}-motoneurons.

Activity changes of α and γ-motoneurons

Dog

With the conduction velocity borders for motoneurons (Fig. 1). mean activities from sweeps of 0.2 s duration were calculated by replaying sweep by sweep from the tape. There was no effort to identify monosynaptic responses. Probably they are also difficult to identify because of their suppression by anaesthesia. All efferent activity was averaged. The recordings were made from a dog nerve root level comparable with the lower sacral range in humans. Because of the anal catheter giving rise to a sustained stretch reflex of the anal sphincters, the activity of a few oscillatory firing sphincter motoneurons (Schalow 1991b) will be intermingled with

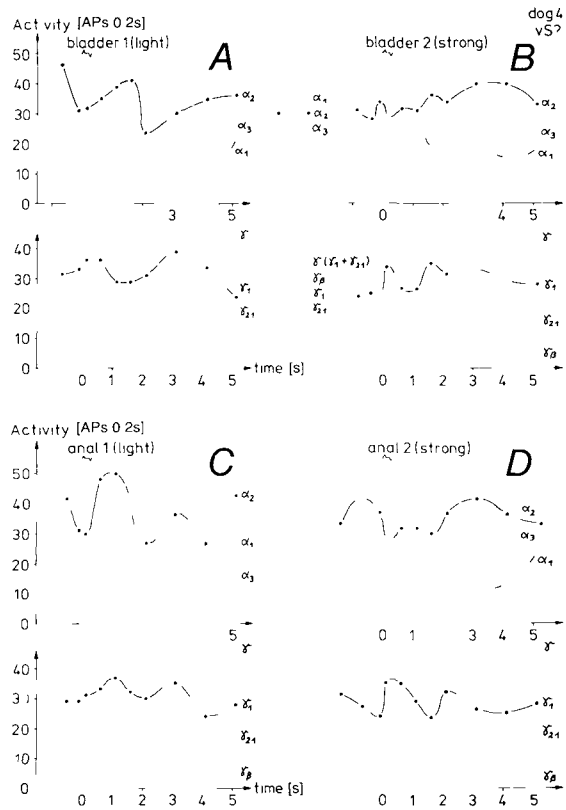

Figure 2. Activity levels of extrafusal and intrafusal motoneurons following strong and light bladder and anal catheter pulling. The splitting of the γ-motoneuron activity into γ_1 and γ_{21} is based on their different time dependences. Activity levels were calculated from histograms of sweeps of 0.2 s duration. Some stimulation appears already before the indicated stimulus because of the handling during the fixation of the catheters.

the activity of the occasional active motoneurons. The sphincter motoneurons will probably be outnumbered by the motoneurons to the tail.

Fig. 2 shows the activity of the different α and γ-motoneuron groups following bladder and anal catheter pulling. There are similarities between the activity changes of a light bladder and a light anal catheter pulling, and between a strong bladder and a strong anal catheter pulling, whereas there are great differences between a light and a strong bladder, and a light and a strong anal catheter pulling. The activity changes following stimulation are rapid at the beginning and become smoother 2 to 3 s later. The α_1-motoneuron activity increased quickly (Fig. 2*B*) following a strong bladder catheter pulling. Probably, this indicates a

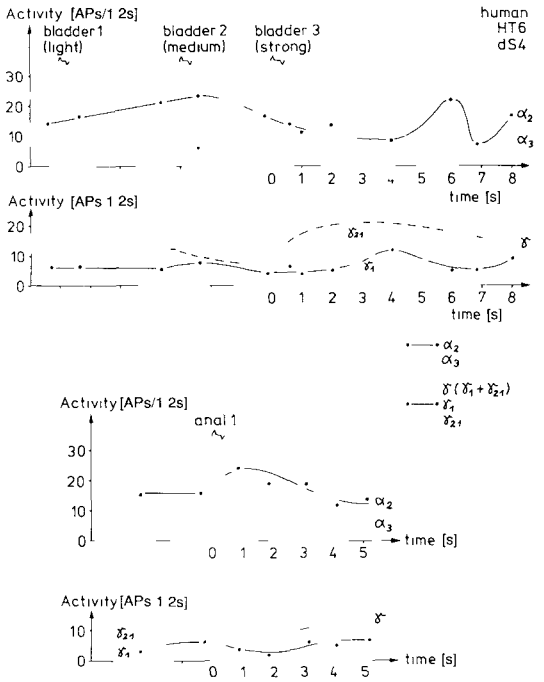

Figure 3. Activity levels of extrafusal (α_2, α_3) and intrafusal (γ_1, γ_{21}) dorsal root motoneurons following bladder and anal catheter pulling. The group velocity ranges are taken from Fig. 5*B* of a previous paper (Schalow and Barth 1992). The activity levels were calculated from conduction velocity frequency distribution histograms of sweeps of 1.2 s duration. The moment of bladder and anal catheter pulling is indicated.

contribution from a monosynaptic response. For a light bladder catheter pulling, the α_1-motoneuron activity was reduced (Fig. 2*A*). From patients it is known that strong urinary bladder catheter pulling is painful. Probably, the dog contracted numerous muscles because of the pain afferent input. Patients further report the wish to micturate with light bladder catheter pulling. The dog probably reduced muscle strength with light pulling. Similar arguments hold for the wish to defecate and the contraction of muscles, because of pain afferent input when pulling the anal catheter with different strength.

The problem with this dog recording is that the motoneurons of the root probably innervate tail muscles, sphincters (mainly by α_2-motoneurons, Schalow 1991a, b, c), muscle structures similar to the pelvic floor, and some leg muscles. The measured activity levels are therefore a sum of the activities of motoneurons with different functions. The recording situation is too complex to safely extract

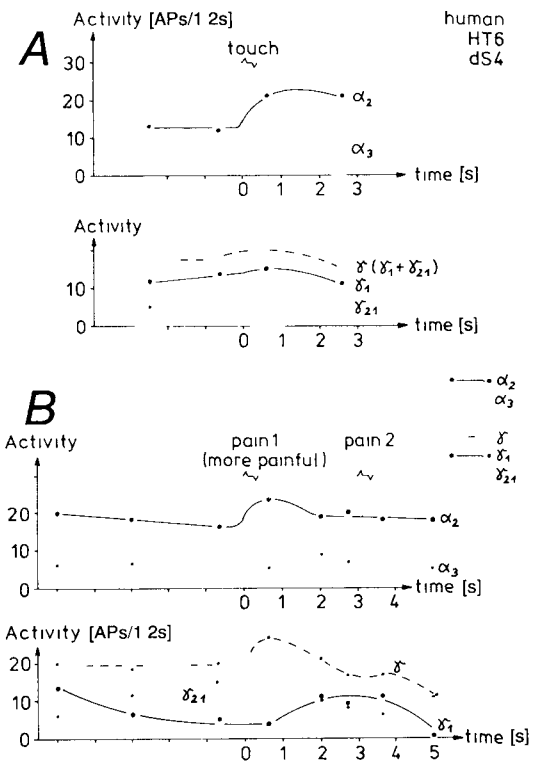

Figure 4. Activity levels of motoneurons following touch and pin-prick (pain). For further details see legend to Fig. 3.

functions from single motoneuron pools. As will be shown below, the recording situation is different in humans. Functions of motoneurons innervating the tail will not be mixed with those of sphincter motoneurons, because humans have no tail. The contribution from motoneurons innervating leg muscles is also small since α_1-motoneurons, which are probably an indicator of leg muscle innervation, were very little present in that root.

As can be seen from Fig. 2, the activities of the γ_{21}, γ_1 and γ (γ_{21} +γ_1) - motoneuron groups changed quite differently. The splitting of the large γ -peak into the contributions from the γ_{21} and γ_1 groups (Fig. 1) is therefore justified.

The activity levels of the γ_β-motoneurons in Fig. 2 do not change very much. No functional properties of them can be extracted from the measurements. From the position of the γ_β-motoneurons in the conduction velocity distribution histogram of Fig. 1 they even seem to belong to the class of α-motoneurons

Human

Fig. 3 shows the activity changes of α and γ-motoneurons in a human dorsal S4

root. The behaviour of α_1-motoneurons could not be demonstrated because this root contained only few α_1-motoneurons (Schalow 1991a). Since the activity levels were low (maybe, because of a partial spinal shock, probably occurring in fresh HTs), sweeps of 1.2 s duration were used to obtain sufficiently high activity levels. As can be seen from Fig. 3, the activity changes are not as complex as in the dog, and the first changes are missing. Monosynaptic responses were not activated or were not present (Schalow 1991c). Since it has been shown in cat (Jankowska et al. 1978) that sphincteric motoneurons show no monosynaptic response, this indicates that the motoneurons in the root mainly innervated sphincters and functionally associated perineal muscles. Such an interpretation is supported by the functions of the afferents and by the existence of a sphincteric α_2-motoneuron of the external urethral sphincter in this root (Schalow 1991a, b, c). Single functional responses of α and γ-motoneurons can also be seen following touch and pain (Fig. 4). The different behaviour of α_2 and α_3-motoneurons following medium and strong bladder catheter pulling can be seen in Fig. 3*A*, mimicking the wish to micturate (medium pull) and the application of pain (strong pull). The important difference is the activation of the γ_{21}-motoneurons. Long lasting activation of the γ_{21}-motoneurons (Fig. 3*A*) resulted in a cumulative reaction (Granit et al. 1957), since the sondary spindle afferents increased strongly their activity for more than 10 min (Schalow 1991c, 1992). From Figs. 3 and 4 it can be seen that the α_2-motoneurons show a more specific response than the α_3-motoneurons. For further analysis and discussion of the different responses see Schalow 1991c.

A more specific recruitment following different stimulations can be expected for the α_2-motoneurons than for the α_3-motoneurons. Similarly, the dynamic γ_1-motoneurons probably show a more specific recruitment than the static γ_{21}-motoneurons. This will be shown for dogs in the next section.

By comparing the responses following bladder and anal catheter pulling in dogs (Fig. 2) and humans (Fig. 3), it can be seen that measurements in the dog cannot substitute for measurements in humans.

Recruitment within the groups of γ_1, α_2 and α_3-motoneurons

Dog

Fig. 5 shows frequency distribution histograms of single conduction velocities from sweeps of 0.2 s duration 0, 1, 2, 3, 4 and 5 s following bladder catheter pulling. With the conduction velocity borders of single motoneuron groups (Fig. 1) the velocity distributions of the γ_1, α_2 and α_3-motoneurons are marked. It can be seen from Fig. 5 that among the γ_1 and α_2-motoneurons the fibres with low or high conduction velocities are preferentially activated at different times. At zero time, i. e. the time interval 0 to 0.2 s following stimulation, more fibres with a low conduction velocity are activated. This stage is indicated with arrows pointing to lower velocity values (to the left). At time 1, the time between 1.0 and 1.2 s,

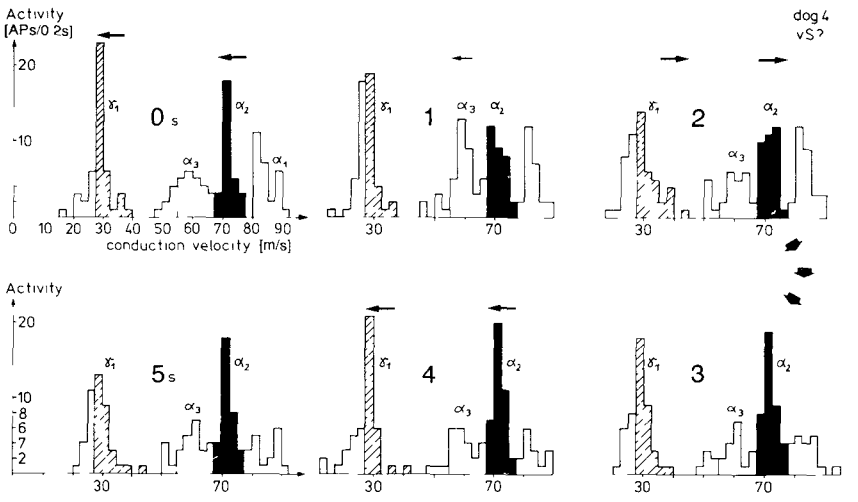

Figure 5. Occurrence of changes of single conduction velocities within the group of γ_1, α_2 and α_3-motoneurons following strong bladder catheter pulling. Group conduction velocity ranges taken from Fig. 1*B*. The figures 1, 2, 3, 4 and 5 indicate time following stimulation. Arrow direction (← ; →) on top of the histograms indicate stages in which motoneurons of a certain group with low or high conduction velocity are preferentially activated, as can be calculated from the histograms. The histogram for prior to 0 s showed no preferential activation, it was similar to the 5 s histogram. γ_1 -velocities (cross hatched), α_3-velocities (dotted), α_2-velocities (filled).

there is no priority to higher or lower velocities. At time 2 (2.0 to 2.2 s) γ_1 and α_2-motoneurons with higher conduction velocities are more activated (arrows point to the right in Fig. 5). At time 3 (3.0 to 3.2 s) the medium velocities are more activated. At time 4 (4.0 to 4.2 s) again the fibres with low conduction velocities are more activated (arrows point to the left). Five s following stimulation, there is no priority of occurrence of low or high velocities. The velocity distribution for time 1 s before stimulation, not shown in Fig. 5, had a similar shape than that for time 5. It is concluded that upon bladder catheter pulling the γ_1 and α_2-motoneurons with low conduction velocities are activated before the motoneurons with higher conduction velocities. However, the recruitment changes in γ_1 and α_2-motoneurons continue until the full response to the afferent input is carried out.

The recruitment of α_3-motoneurons is not as pronounced. There is a preferential occurrence of the low conduction velocities at time 1 (small arrow). The α_3-motoneurons are recruited later than the α_2-motoneurons.

In Fig. 4 of a previous paper (Schalow and Barth 1992), the group conduction velocities were correlated with the group nerve fibre diameters. It could be shown

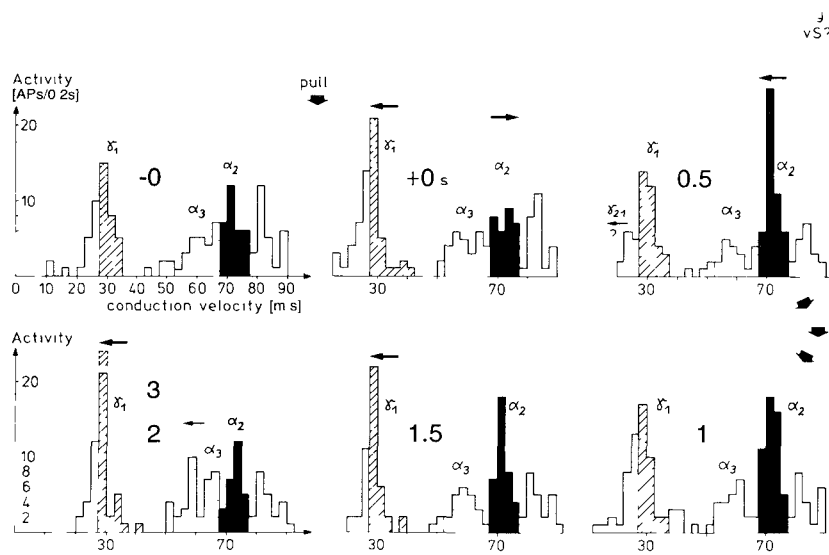

Figure 6. Occurrence of changes of single fibre conduction velocities within the groups of γ_1, α_3 and α_2-motoneurons following light anal catheter pulling. For further explanation see legend to Fig. 5. The 3 s histogram is partly contained in time 2 (dashed lines).

that groups with larger nerve fibre diameters had higher conduction velocities. Since axon diameter, myelin sheath thickness, and conduction velocity increase continuously it will also hold within nerve fibre groups that a thicker nerve fibre conducts on the average faster than does a thinner fibre. Fig. 5 thus illustrates that in each group motoneurons with thinner axons are activated first.

The result of the bladder stimulation shown in Fig. 5 is identical with that presented in Fig. 2*B*. By comparing Fig. 5 with Fig. 2 it can be seen, that the recruitments of motoneurons in this measuring situation are not very well correlated with the changes of the activity levels.

Fig. 5 shows further that the recruitment of the γ_1 and α_2-motoneurons runs in parallel as if they were co-recruited. Since the record shown was taken at approx. 30mm from the spinal cord, delay differences from the different group conduction velocities of α and γ-motoneurons are in the range of 1 ms, and cannot be seen on this time scale. The activation levels of the γ_1-motoneurons behave similarly to those of the α_2-motoneurons (Fig. 2). Therefore, the question arises whether co-recruitment of the γ_1 and α_2-motoneurons is a standard event, or whether the γ_1-motoneurons can sometimes be co-activated with the α_2-motoneurons and sometimes not. Fig. 6 shows distribution histograms of single conduction velocity frequencies at every 0.5 s, and following a light anal catheter pulling. At time

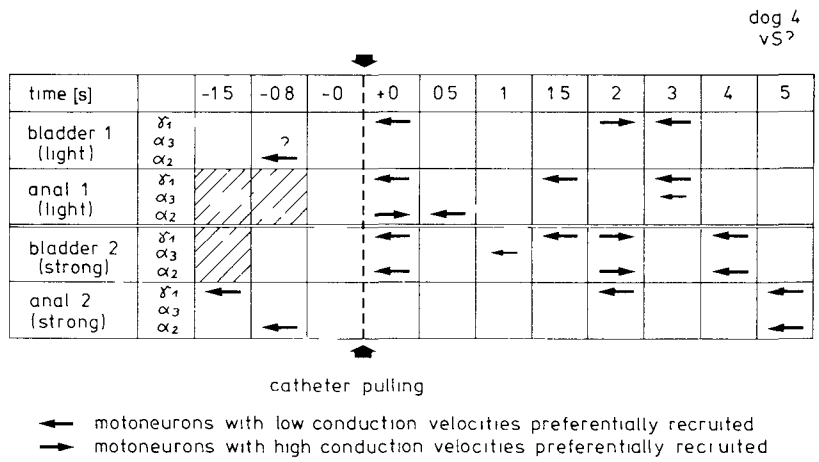

Figure 7. Prefential occurrence of low (←) and high (→) conduction velocities of single γ_1, α_3 and α_2-motoneurons (Figures 5 and 6) in dependence on time in seconds. Minus time indicates time before stimulation. Cross-hatched areas are intervals when no measurement was done. Not all stages of the preferential occurrence of high conduction velocities are indicated.

0, 0 to 0.2 s following anal catheter pulling, slowly conducting γ_1-motoneurons, but not the slowly conducting α_2-motoneurons are activated. They are only activated at time 0.5, i.e. between 0.5 and 0.7 s following stimulation. At time 1.5 s, the slowly conducting γ_1-motoneurons are activated again, but again not the α_2-motoneurons. To get more information about the co-recruitment all values shown in Fig. 2 were examined for recruitment and drawn into Fig. 7. It can be seen from Fig. 7 that there is γ_1-α_2-motoneuron co-recruitment following a strong bladder catheter pulling, and none following a light bladder catheter pulling. However, it should be remembered that strong bladder catheter pulling produces pain and light bladder catheter pulling produces something like a wish to micturate. In the first case, the sphincters and the pelvic floor muscles will be contracted, whereas in the second case they probably will be relaxed. Somehow similar arguments will hold for strong and light anal catheter pulling. Fig. 7 shows that the γ_1 (intrafusal, dynamic), the α_2 and the α_3-motoneuron (extrafusal) systems are activated, according to size, independent of each other. But with strong bladder catheter pulling the γ_1 and α_2-motoneuron systems were activated at the same time at time 0 and time 4. Even in this co-activated situation the γ_1-system is activated once more in between at time 1.5 s (bladder 2, time 1.5; anal 1, time 1.5). This behaviour points towards a synchronization of the γ_1 and the α_2-motoneuron system. Thus, the γ_1 and α_2-motoneuron systems synchronize or not, depending on the composition of

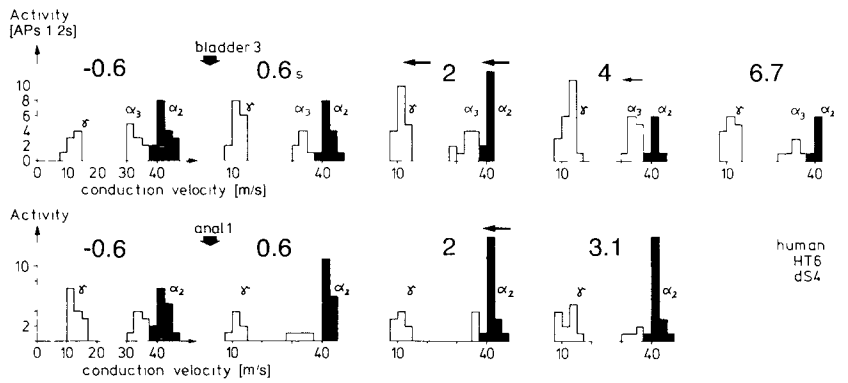

Figure 8. Occurrence of changes of single fibre conduction velocities within the groups of γ_1, α_3 and α_2-motoneurons following strong bladder and anal catheter pulling. Conduction velocity ranges are taken from Fig. 5*B* of a previous paper (Schalow and Barth 1992). Figures −0.6, 0.6, 2, 4, 6.7 and 3.1 indicate the time in seconds following stimulation. Arrows (←) on top of the histograms indicate the interval in which motoneurons with low conduction velocities in a group are preferentially activated. -0.6 means 0.6 s before stimulation. Sweep length for the histograms: 1.2 s.

the afferent input following physiologic stimulation.

One drawback of the recording from the dog sacral nerve root was that the measurements included mixed functions. It will be interesting to examine recruitment in the human root in which primarily only sphincter functions are contained.

Human

Fig. 8 shows distribution histograms of single conduction velocity frequencies from sweeps of 1.2 s duration, 0.6 s before and 0.6 s, 2 s and at other times after bladder and anal catheter pulling. To analyse recruitment the conduction velocity borders of α_2 and α_3-motoneurons were taken from Fig. 5*B* of a previous paper (Schalow and Barth 1992). It can be seen from Fig. 8 that the α_2-motoneurons with low conduction velocities are not activated directly following bladder or anal catheter pulling. At time 0.6 s, 0 to 1.2 s after stimulation, low conduction velocities are not preferentially activated. Only at time 2, 1.4 to 2.6 s after stimulation, α_2-motoneurons with low conduction velocities were preferentially activated (the arrows in Fig. 8). At later times following bladder catheter pulling, there was again no preferential activation. However, as can be seen from Fig. 3, approx. 4 s following anal catheter pulling, and approx. 8 s following strong bladder catheter pulling, the motoneuron response was already completed. In the α_2-motoneuron system, the motoneurons with low axonal conduction velocity were activated first.

The γ-motoneuron peak in Fig. 8 could also be split up into γ_{21} and γ_1-motoneurons. Because of the low activity, the variation was too large to allow safe conclusions. However, following bladder catheter stimulation, at time 2 the γ_1-motoneurons show some preferential activation for low conduction velocities. It seems therefore that also in humans there is some co-recruitment of the γ_1 and α_2-motoneurons.

From Fig. 8 (following bladder catheter pulling) it can be seen that there is some preferential activation of slowly conducting α_3-motoneurons at time 4. The recruitment speed of the α_3-motoneurons is, as in the measurements on the dog (Fig. 5 and 6), lower than that for the α_2-motoneurons.

By comparing the recruitment changes seen in Fig. 8 (bladder 3) with the activity level changes shown in Fig. 3*A*, it can be seen that within the measurement accuracy the preferential activation of low conduction velocities at time 2 of α_2-motoneurons falls very roughly together with the peaks of activity level changes. Also, preferential activation of low conduction velocities of α_3-motoneurons occurs at time 4, about at approx. the same time interval when the activity is highest. Thus, the recruitment of low conduction velocities falls roughly together with the peaks of activity changes. Better measurements are needed for more definite conclusions to be drawn.

Probably, the missing of mono- and oligosynaptic pathways resulted in a slowlier recruitment of γ_1, α_2 and α_3-motoneurons in comparison with those measured in the dog.

Comparison of recruitment between dogs and humans

Even though the recordings from the dog and the human models were both made from lower sacral roots, it can be seen from Fig. 2 and Figs. 3 and 4 that the activity level changes in the dog were different from those in humans. Also, the recruitment speed was different (Figs. 5 and 8). The interpretation is that the physiologic functions are probably similar in dogs and humans. The differences follow from different measuring situations. In the dog, tail or leg functions were probably represented mainly in the measured sacral roots, and main contributions will have come from the mono- and oligosynaptic pathways. In humans, sphincter function was most likely mainly represented in dorsal root S4 and the main contribution will have come from polysynaptic pathways since sphincter-motoneurons show no monosynaptic response in cats (Jankowska et al. 1978) and humans (Schalow 1991c). Since sphincter motoneurons respond to the constant stretch of the anal canal and high bladder fillings to secure continence with a high firing rate in the oscillatory firing mode, the activities of the 2 oscillatory firing motoneurons were subtracted in the case of humans. No care was taken of oscillatory activity in the measurements on dogs.

The different recruitment and the different activity changes in dogs and hu-

mans probably resulted from the different motoneuron pool composition of the nerve roots, and the differences in the mono-, oligo-, and polysynaptic pathways from the afferents to the motoneurons in the spinal cord. A direct comparison of the two species is only possible if one records from comparable motoneuron pools, and this was not possible in this case. Also, male dogs have a different micturition behaviour: "They are running from tree to tree". An additional problem arises when comparing the results of measurements on dogs and humans: namely, how comparable are the afferent inputs between dogs and humans. Stretch, flow, and mucosa afferents (Schalow 1991a) may be similar in dogs and humans, but the skin afferents are not. In humans, skin afferents also contribute to sensing of the anal canal (Schalow 1991a, Schuster 1968).

Discussion

Changes in discharge rats and changes in recruitment of conduction velocities within different motoneuron types have been shown to occur in dogs and humans (Figs. 2 to 8). These measurements, in connection with the different repetitive activities (Hodgkin 1948, Schalow 1991a), probably different spinal oscillators (Schalow 1991b, c), and the different passive membrane properties (Fleshman et al.1981, Gustafsson and Pinter 1984) for different motoneuron types, support the classification of motoneurons into different groups (Burke et al. 1973, Desmedt 1983, Schalow 1991a, b, c).

The possible co-recruitment of the dynamic intrafusal γ_1-motoneurons with the α_2-motoneurons (FR-type) seems to be a new observation, and needs further clarification in connection with the γ_1–α_2 co-activity (Prochazka and Hulliger 1983, Schalow 1991c).

Recruitment of new motoneurons in a motoneuron pool of a certain function following stimulation is paralleled by activity changes of already active motoneurons. If it is recorded from different motoneuron pools, as in the measurements on the dog, the activity changes and the recruitment changes of the slower and the faster conducting, γ_1, α_2 and α_3-motoneurons need not to be identical as it was the case in the measurements on the dog. In humans, where recording was mainly from one motoneuron pool, the activity increases occurred at approx. the same time as the maximum recruitment of the slowly conducting axons within the γ_1, α_2 and α_3-motoneuron groups.

Figures 5, 6 and 7 show with the periodic changes in the recruitment of slower and faster conducting γ_1 and α_2-motoneurons, that recruitment is a rather dynamic process: motoneurons with different conduction velocities in a certain group are activated repeatedly for longer lasting responses. This is likely due to nutritional and resting aspects of the innervated muscle fibres. Recruitment therefore seems to occur when in addition, certain motoneurons are activated constantly for

a certain time following additional afferent input. The first recruitment increase in the group of α_2-motoneurons follows the conduction velocity, i.e. slowlier conducting motoneurons are activated first (size principle). The same holds for the γ_1-motoneurons and also for the α_3-motoneurons. That motoneurons can change from the occasional spike mode into the oscillatory firing mode of high activation (Schalow 1991b) is unimportant in this connection, since the additional input was only short, whereas the oscillatory firing mode of motoneurons appears with strong continuing afferent input of a certain kind as in the tonic stretch reflex of the anal sphincter. In a situation of a rather constant low level afferent input before stimulation, it cannot be decided whether certain motoneurons of a certain conduction velocity are always activated, or whether there is an ongoing recruitment change between motoneurons in the same motoneuron group with similar conduction velocities, the same group with different conduction velocities or different groups with different conduction velocities. From efficiency aspects, again a dynamic activation would make more sense than a static one. As indicated by Figure 7, the history of recruitment before stimulation has also to be taken into consideration, i.e. in what recruitment and activation stage is the system under consideration when the additional stimulus is applied.

The recruitment speed has also to be considered. In Fig. 5 the first recruitment of slowly conducting α_2 and γ_1-motoneurons is fast. Most likely, mono- and disynaptic pathways were used for the new activation of slowly conducting axons, even though efferent responses are strongly depressed by the anaesthesia. In Fig. 8 the time until maximum recruitment of slowly conducting α_2-motoneurons took approx. 2 s. Polysynaptic pathways were used, because of the missing of mono- and disynaptic pathways (Jankowska et al. 1978, Schalow 1991c). The recruitment has therefore also to be considered with respect to which spinal interneuron circuits are potentially existing between the afferent fibres and the motoneurons of concern, and which pathways are channeled following the discharge pattern in the afferent fibres in the individual afferent groups.

Figures 5, 7 and 8 show further that the α_3-motoneurons (conducting slowlier than the α_2-motoneurons) reach the highest activation of slowly conducting motoneurons later than do the α_2-motoneurons. In the mono- and disynaptic pathways (Fig. 5) the slowly conducting α_3-motoneurons are highly activated 1 s following stimulation, and in the polysynaptic pathways (Fig. 8) 4 s following stimulation. In Fig. 5, probably the recruitment in the polysynaptic pathways was mixed with the recruitment in the mono- and oligosynaptic pathways. The gradation in the recruitment of the different pathways probably also has to be taken into consideration if mono- and polysynaptic pathways are channelled simultaneously. In the measurement on human sphincteric motoneurons (Fig. 8) the lucky situation seems to exist that no mono- and disynaptic pathways were existing.

In the measurements on the dog (Figs. 5 and 6), no clear recruitment of the

α_1-motoneurons can be seen, even though one would expect an initial recruitment according to the conduction velocity. One explanation is that the time base used for measuring conduction times was too slow, so that the very short conduction times of the α_1-motoneurons were too inaccurate to show clear activation changes among the α_1-motoneurons. Another explanation is that additional α_1-motoneurons were not activated with the additional, mainly interoceptive, afferent input from the bladder catheter pulling. "The dog would not know to which direction to escape (escape reaction: activation also of α_1-motoneurons), if pain is felt in the urinary bladder". The sphincters are mainly innervated by α_2 and a few α_3-motoneurons (Schalow 1991b, Schmidt et al. 1979 (dog)). Therefore, the pulling of the bladder and the anal catheter will stimulate the α_2 and α_3-motoneurons, which innervate the sphincters and the functionally associated pelvic floor muscles.

Efferent responses are probably strongly depressed in HTs because of the spinal shock, even though the reflex activity of the external urethral sphincter recovers much earlier after spinal injury from spinal shock than the rest of the skeletal muscles (Yalla et al. 1977). In patients or dogs the efferent responses will be depressed because of the anaesthesia. However stronger efferent responses can be expected in electrodiagnosis during surgery on paraplegics with complete lesions, where the light anaesthesia mainly serves to put the patient to sleep (no pain is felt in the disconnected parts). If occasionally some monosynaptic pathways to the extremities are represented in the lower sacral roots, monosynaptic responses may occur on the recordings.

Clinical implications

Electrical stimulation

It has been shown that different extra- and intrafusal motoneurons are activated according to size within their motoneuron groups. If the response lasts 5 to 10 s the activation of slowly and fast conducting motoneurons alternates with a period of 3 to 4 s for α_2-motoneurons, and 1.5 to 2 s for γ_1-motoneurons. If the response is continuous, as in the constant stretch reflex of the anal canal, then the α_2-motoneurons fire, in the high activation mode of oscillatory firing, repeatedly with an impulse train of 3 action potential approx. every 160 ms, and α_3-motoneurons with long impulse trains of approx. 40 action potentials every 1.6 s (Schalow 1991b, c). Such specialized activation pattern of highly activated motoneurons, consisting of a short activity phase and a long pause, could give the innervated muscle fibres a short rest to recover. The question arises, what happens if one disregards such activation pattern for very long lasting artificial stimulation such as electrical stimulation of the diaphragm in cervical spinal cord lesions, where the phrenic nerve (the last respiration nerve) is also disconnected from the supraspinal centres. It has been reported that the diaphragm stopped contracting following 5 years of continuous nerve stimulation. Even though neuropathologists have not analysed

the diaphragm for the failure of function at autopsies, it seems that one has to imitate, by electrical stimulation, physiologic patterns. With reduced and alternating stimulation the diaphragm of tetraplegics remained longer active. Separate stimulation of the different intrafusal and extrafusal motoneuron groups is still unsolved. Functional electrical stimulation (FES) (Vodovnik et al. 1978, Kralj et al. 1986) may be one solution. However a better solution may be to stimulate afferent fibres, or even better, the extero- and intero-receptors which activate the phrenic nerve, to make the diaphragm contract in a physiologic manner. A similar physiologic response requires that the interneuron pool with its circuitry of the functionally disconnected spinal cord is undamaged.

Separation of functions, plasticity and possible repair in spinal lesions

It has been shown (Fig. 7) that the γ_1 and the α_2-motoneuron system in the central nervous system (CNS) can co-operate, perhaps by synchronization, and can be activated separately. Such co-activation and separation of functions could be one property of plasticity for relearning functions. It has been reported that if in rats one transposes the nerves or the tendons to antagonistic muscles, the animal is unable to relearn (Sperry 1945), whereas the monkey regains the ability after some time (Sperry 1947), and humans need no time as they can visualize the task (Weiss and Brown 1941). The neuronal readjustment for functions most likely involved reorganization at supraspinal level (Tsukahara 1978). If, for example, nearly all interneurons are destroyed in the human spinal cord, so that mainly only monosynaptic pathways are still functioning, then it will not be possible to still relearn such functions. However, if the interneuron pool is still fully functioning, and if different functions can be coordinated and separated, then supraspinal centres may have the chance to coordinate desired functions by learning, if sufficient descending tract fibres exist or can be reconstructed.

In partial spinal cord lesions it may be possible to get useful function by modifying the spinal cord excitability by pharmacological intervention (Grillner and Dubuc 1988).

In complete spinal cord lesions, dyssynergy of the urinary bladder often occurs (Yalla et al. 1977, Blaivas et al. 1981), which means that the detrusor and the sphincter system are no longer working in a coordinated, antagonistic, way. The reason is unclear. The brain stem micturition centre probably functions well, whereas the functionally disconnected sacral micturition centre most likely does not. Two possible reasons for the "spasticity", or dyssynergy, of the bladder are that the interneuron pool is partly destroyed, or the afferent input from the bladder is processed in an unbalanced way because of nerve fibre sprouting and other readjustments (Burke 1988, Grüninger 1989).

The cutting of lower dorsal sacral roots in paraplegic patients, which also destroys the potency of the patient, and implanting electrodes for electrical sti-

mulation (Brindley et al. 1986), indirectly implies that the interneuron pool is irreversible damaged, so that the function of the sacral spinal cord is lost. However it may well be that dysfunction is due to an unbalanced processing of the afferent input from the bladder because of the sprouting of the afferents to synapses of the former descending tract fibres and the loss of coordinating functions from the brain stem and supraspinal centres. It might be possible to restore functions by partial retrograde reinnervation with intercostal nerve fibres of sufficient number and function from above the lesion into dorsal and ventral sacral roots (Schalow 1991b). It also seems that afferent fibres, in the neighbourhood of embryonic nervous tissue, can cross the PNS-CNS transition zone and regenerate into the CNS in rats (Kliot et al. 1988).

The main task for the time being is to measure with this new method of single unit potential recording on dorsal and ventral S4 roots, where mostly sphincter and detrusor functions are represented (mostly in S3 and S4), to find out the reason for the dyssynergy at the level of neurons, in order to develop precise strategies for the repair. Since patients die of the bladder dyssynergy because of a high pressure in the bladder and infections, something has to be done. Perhaps, sacral root stimulators should preferentially be implanted to older patients to leave younger patients with a higher neuronal plasticity a possibly better future.

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References

Bawa B., Binder M.D., Ruenzel P., Henneman E. (1984): Recruitment of motoneurons in stretch reflexes is highly correlated with their axonal conduction velocity. J. Neurophysiol. **52,** 410—420

Blaivas J.G., Sinha H.P., Zayed A.A.H., Labib K.B. (1981): Detrusor-external sphincter dyssynergy: A detailed electromyographic study. J. Urol. **125,** 545—548

Brindley G.S., Polkey C.E., Rushton D.N., Cardozo L. (1986): Sacral anterior root stimulation for bladder control in paraplegia: the first 50 cases. J. Neurol. Neurosurg. Psychiat. **49,** 1104—1114

Burke D. (1988): Spasticity as an adaptation to pyramidal tract injuries. In: Advances in Neurology, Vol. 47: Functional Recovery in Neurological Disease (Ed. S.G. Waxman) pp.401—423, Raven Press, New York

Burke R.E., Levine D.N., Tsairis P., Zajac F. (1973): Physiological types and histochemical profiles in motor units of cat gastrocnemius. J. Physiol. (London) **234,** 723—748

Desmedt J.E. (1983): Size principle of motoneuron recruitment and the calibration of muscle force and speed in man. In: Motor Control Mechanisms in Health and Disease (Ed. J.E. Desmedt) pp. 227—251, Raven Press, New York

Fleshman J.W., Munson J.B., Sypert G.W., Friedman W.A. (1981): Rheobase, input resistance, and motor unit type in medial gastrocnemius motoneurons in the cat. J. Neurophysiol. **46,** 1326—1338

Granit R., Pascoe J.E., Steg G. (1957): The behaviour of tonic α and γ motoneurons during stimulation of recurrent collaterals. J. Physiol. (London), **138,** 381—400

Grillner S., Dubuc R. (1988): Control of locomotion in vertebrates: Spinal and supraspinal mechanisms. In: Advances in Neurology, Vol. 47: Functional Recovery in Neurological Disease (Ed. S.G. Waxman) pp. 425—453, Raven Press, New York

Grüninger W. (1989): Spinale Spastik. Ueberreuter Wissenschaft, Wien, Berlin

Gustafsson B., Pinter M.J. (1984): Relation among passive electrical properties of lumbar α-motoneurons of the cat. J. Physiol. (London) **356:** 401—431

Herdman J., Reiners K., Freund H.-J. (1988): Motor unit recruitment order in neuropathic disease. Electromyogr. Clin. Neurophysiol. **28,** 53—60

Hodgkin A.L. (1948): The local electric changes associated with repetitive action in a non-medullated axon. J. Physiol. (London) **107,** 165—181

Jankowska E., Padel Y., Zarzecki P. (1978): Crossed disynaptic inhibition of sacral motoneurons. J. Physiol. (London) **285,** 425—444

Kanda K., Desmedt J.E. (1983): Cutaneous facilitation of large motor units and motor control of human fingers in precision grip. In: Motor Control Mechanisms in Health and Disease (Ed. J.E. Desmedt) pp. 235—261, Raven Press, New York

Kernell D. (1983): Functional properties of spinal motoneurons and gradation of muscle force. In: Motor Control Mechanisms in Health and Disease (Ed. J.E. Desmedt) pp. 213—226, Raven Press, New York

Kliot M., Smith G.M., Siegel J., Tyrell S., Silver J. (1988): Induced regeneration of dorsal root fibres into adult mammalian spinal cord. In: Current Issues in Neural Regeneration Research (Eds. P.J. Reier, P. Bunge, F.J. Seil) pp. 311—328, A.R. Liss. Inc., New York

Kralj A., Bajd T., Turk R., Benko H. (1986): Posture switching for prolonging functional electrical stimulation standing in paraplegic patients. Paraplegia **24,** 221—230

Langhorst P., Schulz G., Lambert M. (1986): Integrative control mechanisms for cardiorespiratory and somatomotor functions in the reticular formation of the lower brain. In: Cardiorespiratory and Cardiosomatic Psychophysiology (Eds. P. Grossman, K.H. Janssen, D. Vaitl) pp. 9—39, Plenum Publishing Corporation

Prochazka A., Hulliger M. (1983): Muscle afferent function and its significance for motor control mechanisms during voluntary movements in cat, monkey, and man. In: Advances in Neurology, Vol. 39, Motor Control Mechanisms in Health and Disease (Ed. J.E. Desmedt) pp. 93—132, Raven Press, New York

Schalow G. (1989): Efferent and afferent fibres in human sacral ventral nerve roots: basic research and clinical implications. Electromyogr. Clin. Neurophysiol. **29,** 33—53

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 human. Electromyogr. Clin. Neurophysiol. **31,** 223—241

Schalow G., Barth H. (1992): Group conduction velocities and nerve fibre diameters of α and γ-motoneurons from lower sacral nerve roots in dog and human. Gen. Physiol. Biophys. **11,** 85—99

Schalow G. (1992): Ventral root afferent and dorsal root afferent fibres in lower sacral nerve roots in dog and human . Gen. Physiol. Biophys. **11,** 123–131

Schmidt R.A., Bruschini H., Tanagho E.A. (1979): Urinary bladder and sphincter responses to stimulation of dorsal and ventral sacral roots. Invest. Urol. **16,** 300—304

Schuster M.M. (1968): Motor action of rectum and anal sphincters in continence and defecation. In: Handbook of Physiology, Section 6, Alimentary Canal, Volume IV, Mobility (Ed. W. Heidel) pp. 2121—2146, Amer. Physiol. Soc., Washington D.C.

Sperry R.W. (1945): The problem of central nervous reorganization after regeneration and muscle transposition. Quart. Rev. Biol. **20,** 311—369

Sperry R.W. (1947): Effect of crossing nerves to antagonistic limb muscles in monkey. Arch. Neurol. Psychiat. (Chicago) **58,** 452—473

Tsukahara N. (1978): Synaptic plasticity in the red nucleus. In: Neuronal Plasticity (Ed. C.W. Cotman) pp. 113—130, Raven Press, New York

Vodovnik L., Kralj A., Stanic U., Acimovic R., Gros N. (1978): Recent applications of functional electrical stimulation to stroke patients in Ljubljana. Orthoped. **131,** 64—70

Weiss P., Brown P.F. (1941): Electromyographic study on recoordination of leg movements in poliomyelitis patient with transposed tendons. Proc. Soc. Exp. Biol. Med. **48,** 384—387

Yalla S.V., Rossier A.B., Fam B.A., Gabilondo F.B., Benedetto M., Gittes R.F. (1977): Functional contribution of autonomic innervation to urethral striated sphincter: studies with parasympathomimetic, parasympatholytic and alphaadrenergic blocking agents in spinal cord injury and control male subjects. J. Urol. **117,** 494—499

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