Ventral Root Afferent and Dorsal Root Efferent Fibres in Dog and Human Lower Sacral Nerve Roots

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Abstract. Two pairs of wire electrodes were used to record single afferent action potentials from ventral roots and single efferent action potentials from dorsal roots of dogs and humans.

A human lower sacral ventral root contained about 20 to 30% afferents among fibres with a diameter larger than 5 μ m; a comparable ventral root of a dog contained about 1% afferents. Human S3, S4 and S5 dorsal roots contained 3, 18, and 20 to 30% efferent fibres respectively; a comparable dorsal root of the dog contained less than 1% efferent fibres.

Primary and secondary muscle spindle afferents, Golgi tendon organ afferents, and afferents from the mechanoreceptors of the urinary bladder and anal canal mucosa were activated in a dog ventral root by pulling bladder and anal catheters. Their peak group conduction velocities were 82, 57, 71 and 18 m/s at 34 °C respectively. The dog afferents conducted more than 30% faster than did comparable human nerve fibres.

By strongly pulling the bladder catheter, the static human dorsal root γ_{21} motoneurons increased their activity for about 7 s which in turn strongly increased the dorsal root spindle afferent activity for more than 10 min; the human static intrafusal γ -motoneurons seemed to show cumulative properties.

Key words: Dog — Human — Ventral root afferents — Dorsal root efferents — Single fibre action potentials — Conduction velocities

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Introduction

Ventral root afferents were shown to be present in animals and humans (Coggeshall et al. 1975, Frykholm et al. 1953, Hosobuchi 1980, Schalow 1989, Voorhoeve and Zwaagstra 1984). Also dorsal root efferents seemed to exist (Schmidt et al. 1979, Sherrington 1987). Even though their existence was denied later (Coggeshall 1980), dorsal root efferents were demonstrated in humans (Schalow and Lang 1989). The measurements presented in this paper suggest that dorsal root efferents also exist in dogs. Since only few afferents exist in dog ventral roots, and very few efferents in dog dorsal roots, these fibres are not as useful for research as those in humans. It will be shown in this paper that the afferent fibres in dog ventral roots provide further information about spindles, Golgi tendon organ, and mucosa afferents. The efferents in a human dorsal root supply further information about the relationship between static γ -motoneurons and secondary spindle afferents.

Materials and Methods

The methods and the clinical material are the same as described in previous papers (Schalow and Barth 1992, Schalow 1992).

Results

Ventral root afferents in dogs

Fig. 1A shows a lower sacral ventral root recording containing an afferent action potential (AP) besides efferent APs. The efferent APs could be identified as being conducted in γ_{22} and α_2 -motoneurons since they were conducted within the velocity ranges for γ_{22} and α_2 -motoneurons. The conduction velocity distribution histogram with the velocity ranges was presented in the previous papers (Schalow and Barth 1992, Schalow 1992). By comparing the conduction velocity of the afferent AP with the conduction velocity frequency distribution histogram of Fig. 1B, the AP could be identified as being conducted in a primary spindle afferent fibre. In Fig. 1Ba the primary (SP1) and secondary spindle afferent conduction velocities (SP2) were identified by their continuous occurrence. The M-peak occurred only after bladder catheter pulling. This peak is therefore interpreted as belonging to mechanoreceptor afferents (M) from the mucosa of the urinary bladder and urethra; this conclusion is based on a comparison of its velocity with the velocities of human skin, bladder, and spindle afferents (Schalow 1991a). The velocity distribution histogram upon anal catheter pulling (Fig. 1Bb) shows similar peaks, and an additional peak. Since this additional peak occurred only upon anal catheter pulling it is interpreted as being due to the activity of the Golgi tendon organ afferents because rather strong anal catheter pulling will stretch the sphincters and



Figure 1. A. Sweep piece of extracellularly recorded afferent (SP1) and efferent (γ_{22}, α_2) action potentials (APs) from a ventral sacral nerve root of dog 4. The conduction times with their corresponding velocities (conduction distance = 8mm) are indicated between traces a (proximal electrode pair) and b (distal pair). The APs are labeled according to the group they belong to (see conduction velocity distribution histograms in *B* and Fig. 2 of Schalow and Barth 1992. B. Conduction velocity frequency distribution histograms of 20 sweeps of 0.2 s duration shown partly in *A*. The distribution peaks are labeled according to the group they most likely represent. The mucosal afferents were only active upon the pulling of the catheters. The Golgi tendon organ afferent activity *Bb* occurred only in response to strong anal catheter pulling in the time interval between 0.8 s before and 1.5 s after the pulling.

pelvic floor muscles.

Upon catheter pulling no transiently occurring velocities of fast conducting afferents appeared (Fig. 1*B*). This means that no rather fast conducting skin afferents were stimulated by pulling the catheters. In comparison with human data (Schalow 1991a) this means that this sacral root was from a level comparable to human S3 level at which no skin afferents were stimulated with bladder and anal catheter pulling. Around the meatus of the urethra and the anal canal there seem to be no skin receptors of the S3 dermatome.

Fig. 2 shows activity changes in a lower sacral dorsal root upon anal catheter pulling. In Fig. 2A a piece of recording is shown, and in Fig. 2B the corresponding conduction velocity distribution histogram of the whole sweep. In the velocity ranges of spindle and Golgi tendon organ afferents (Fig. 1B) the activity is increased (Fig. 2Bb) indicating that these afferents had been stimulated. Mucosal afferents seem not to be activated very much.

By comparing Fig. 1Bb with Fig. 2Bb and calculating the velocities it can be seen that the dorsal root afferent activity was about 80 (4×20) times higher than



Figure 2. A. Sweep piece of afferent APs from a sacral dorsal nerve root of dog 4. Conduction times and conduction velocities are indicated. SP1-Ap retouched. B. Conduction velocity distribution histogram of two 0.2 s sweeps, partly shown in A, with no stimulation (Ba) and following anal catheter pulling (Bb).

the ventral root afferent activity. The number of afferents in the sacral ventral root was therefore rather low. It was very roughly in the range of 1% for fibres with conduction velocities higher than 15 m/s.

The peak group conduction velocity of primary spindle afferents was about 82 m/s, that of secondary spindle afferents, Golgi tendon organ afferents, and of the afferents from the mechanoreceptors of the mucosa about 57, 71 and 18 m/s respectively at about 34° C. All measured values are summarized in Table 1 of Schalow and Barth (1992) together with the peak conduction velocity values of the different efferent fibre groups.

Dorsal root efferents in dogs

On the recording shown on Fig. 3 an efferent AP can be seen besides many afferent APs. According to the conduction velocity and the group conduction velocities of intrafusal motoneurons (Schalow and Barth 1992, Schalow 1992) this is probably an AP from a γ_1 -motoneuron. Since there was no activity for 1.5 ms before this efferent-like AP, it can be excluded that this AP stems from an afferent fibre, making a short loop. However, this AP could stem from an afferent fibre having formed a long loop (Coggeshall 1980). Other very unusual afferent pathways could have also existed. Anyway, sometimes efferent-like Aps occurred in the dorsal root recordings. Since dorsal root efferents exist in human lower sacral roots, these efferent-like APs were most likely also from dorsal root efferents. The activity in

Figure 3. Dorsal root efferent AP (γ_1) among afferent APs from a dorsal sacral root of dog 4. Notice that there is no activity directly before the appearance of the efferent AP.



Figure 4. Correlation of activity level changes of secondary spindle afferents (SP2) and γ_1 and γ_{21} -motoneurons (intrafusal) following bladder (A) and anal catheter pulling (B) of a human dS4 root (HT6). The recording shown in B was taken 5 to 10 min later than that in A. Notice that the prolonged activity increase of the γ_{21} -motoneurons (static) following strong bladder catheter pulling substantially increased the SP2-activity for many minutes. Notice also that the scale for the SP2-activity does not start from 0.



dorsal roots as a whole was much higher than that in ventral roots. It is therefore more difficult to safely identify efferent APs in dorsal roots than afferent APs in ventral roots.

Ventral root afferents and dorsal root efferents in humans

It has been demonstrated earlier that ventral root afferents and dorsal root efferents exist in humans (Schalow and Lang 1989, Schalow 1989, Schalow 1991a, Schalow and Barth 1992, Schalow 1992). Since they are often present in the S4 and S5 roots, they can be used for analysing the relationship between afferent and efferent impulse traffic.

Fig. 4 shows the activity changes of secondary spindle afferents in response to γ_1 and γ_{21} -motoneuron activity upon bladder and anal catheter pulling in a dorsal root. There is no γ -motoneuron and no spindle afferent response to light bladder catheter pulling (Fig. 4A). A transient γ -motoneuron and spindle afferent response appeared upon medium bladder (Fig. 4A) and anal catheter pulling (Fig. 4B). Upon strong bladder catheter pulling (Fig. 4A) the γ_{21} -motoneuron activity increased for more than 7 s, which in turn increased the secondary spindle activity (SP2) for more than 10 min. This can be explained by the cumulative action of the static γ -motoneurons (Granit et al. 1957). The very long increased spindle afferent activity changes from parasympathetic fibres cannot be excluded.

The data obtained from dogs allowed a better distinguishing of γ_1 and γ_{21} motoneurons in humans (see Schalow and Barth 1992). This in turn brought out more clearly the cumulative nature of static γ -motoneurons and possibly parasympathetic fibres in this measurement on humans.

Discussion

Comparison of dog and human ventral root afferents and dorsal root efferents

It has been shown earlier that about 20 to 30% of lower human sacral ventral root fibres with a diameter larger than 5μ m were afferent fibres (Fig. 5 in Schalow 1989). The measurements on dogs showed that approx. 1% of the sacral ventral root fibres were afferent. In humans the percentages of dorsal root efferents increased from about 3% in an S3 dorsal root, to 18% in an S4 and to 20 to 30% in a dorsal S5 root (Schalow 1991a). Efferents in the sacral dorsal dog roots were just at the level of detectability. Their percentages are probably much below 1%. A possible explanation for this species difference is that the dog has a tail. The circuitry for the tail movement lies in the conus medullaris and makes the conus thicker and longer. In dogs, the dorsal and ventral rootlets from the medulla are therefore more separated and make a false growing during the development less likely.

As can be seen from Table 1 in Schalow and Barth (1992) and Figs. 1 and 2, the spindle, Golgi tendon organ, and mucosal afferents in dog conducted more than 30% faster than did comparable fibres in humans. Schalow and Barth (1992) also showed that at 34°C the extrafusal motoneurons of dogs conducted 60% (α_3)



Figure 5. Approximate peak values of group conduction velocities (V) (root temperature 36 °C) and group nerve fibre diameters (\emptyset) of afferent and efferent nerve fibres in the cauda equina approx. 3cm distal to the conus medullaris. Human age about 30 years. GO, S1, ST, S2, M = afferents with the corresponding group nerve fibre diameters unknown. M, S2 = possibly the same afferents. The insert shows the shape of the schematic frequency distribution of conduction velocities and nerve fibre diameters, peak value indicated.

to 30% (α_1) faster than did human motoneurons.

Conduction velocities and diameters of human and dog nerve fibres

Fig. 5 shows the conduction velocities and diameters of human nerve fibres so far measured with the single unit potential recording method (Schalow 1991a, 1991b, 1991c, Schalow and Barth 1992). It is assumed that dorsal root efferents and ventral root efferents, and ventral root afferents and dorsal root afferents, belong to the same fibre groups; only some fibres grew through the "wrong" exit of the medulla. The improvement of the conduction velocity - fibre diameter scheme of Fig. 5 compared to that in Schalow (1991a) is that the values for the γ -motoneurons are more exact and that the Golgi tendon organ afferents are fitted. The Golgi tendon organ afferents measured in dogs to have conduction velocities between those for the primary and secondary spindle afferents (Fig. 1B). Further measurements on humans are under preparation to show that the Golgi tendon organ afferents in humans also conduct with velocities intermediate to those of the primary and secondary spindle afferents. There has been no effort to split up the human α_1 -motoneuron group into subgroups because there were only few α_1 -motoneurons in the roots measured.

A velocity – diameter scheme comparable to that in Fig. 5 could also be drawn for dogs using the data from Table 1 in Schalow and Barth (1992). Mean values however require more measurements. So far it seems that the relations between the conduction velocities of the different nerve fibre groups are more consistent than the actual values of the velocities. In humans it was shown that the α_2 motoneurons had about the same conduction velocities as the secondary spindle afferents and the T1 (PC) skin touch afferents (Schalow 1991a). From Table 1 in Schalow and Barth (1992) it can be seen that in dog 2, the secondary spindle afferents also seem to have the same conduction velocity as the α_2 -motoneurons do, whereas in dog 4 the secondary spindle afferents had about the same velocity as the α_3 -motoneurons. More measurements are needed to calibrate the conduction velocity relations between afferents and efferents in dogs.

The identification of group conduction velocities and group nerve fibre diameters (Schalow 1989, 1991a, Schalow and Barth (1992) of the different nerve fibre groups represents a basis for a better understanding of the functions of the human nervous system (Schalow 1991a, 1991b, 1991c, 1992). This, in turn, can help the progress in Restorative Neurosurgery (Schalow 1991b).

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