Single-motor-unit discharge characteristics in human lumbar multifidus muscle

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Abstract

The underlying neurophysiology of postural control of the lower back in humans is poorly understood. We have characterized motor unit (MU) discharge activity in the deep lumbar multifidus (LM) muscle in 9 healthy subjects (20–40 years, 3 females). Bilateral fine wire electrodes were implanted at L4 spinal level using ultrasound guidance. EMG was recorded during spontaneous sitting and standing, and during voluntary force production. Individual MUs were analyzed with regard to instantaneous discharge rate, interspike interval variability, alternation of activity between MUs, and cross correlation between concurrently active MUs quantified by the common drive coefficient (CDC). Significant effects of sitting vs. standing were seen on median discharge rate and interspike interval variability. Median discharge rate in 71 units was 5.4 and 6.9 pps during spontaneous sitting and standing, and 7.4 pps during voluntary force production. Several MUs fired doublets. CDC analysis of 87 MU pairs showed significantly higher common drive in spontaneous than in voluntary activity and significant differences between unilateral and bilateral pairs, although not when spontaneously active in standing. In spite of common drive, MUs were recruited from inactivity to tonic discharge lasting for several minutes without changes in discharge rate in already active MUs, and several instances were documented where activity was rotated between MUs. We argue that this behavior is indicative of self-sustained discharge in LM motoneurons, establishing intrinsic motoneuron properties as a central mechanism for postural control of deep back muscles.

Keywords

Back; motor activity; muscle tonus; motor neurons; electromyography
Introduction

The neurophysiology underlying postural control of the back is poorly understood. In particular, literature on strategies for spontaneous control of muscle tone in healthy human subjects is scarce. This is remarkable, since knowledge of normal motor physiology would also constitute a basis for research of motor physiology in low back pain (LBP), a condition that has substantial impact on individual quality of life and high socio-economic costs (Maniadakis and Gray 2000; Vos et al. 2012).

The deepest part of the paraspinal muscles, in particular the lumbar multifidus (LM), has been postulated to have an important role in postural stability, and LM integrity appears to be important for spinal health (Panjabi 1992; Wilke et al. 1995; Comerford and Mottram 2001). Solid EMG data documenting LM function is however scarce, mainly due to the muscle’s anatomical position which does not allow selective recording of EMG through surface electrodes (Stokes et al. 2003). Probably for the same reason we have not found any previous work documenting long-term intramuscular recordings of single LM motor units (MUs) during unhindered activity.

The LM originates along the spinous process, and its distal attachment is the lateral aspect of the mammillary process or lamina of a vertebra more caudad (Macintosh et al. 1986). Its deepest fascicles are short and span across two vertebrae, whereas the more superficial fascicles have a longer span. The LM is active in extension against resistance and in contralateral rotation, in spite of the short leverage arm of the LM which makes it an unlikely primary rotatory mover (Donisch and Basmajian 1972). A possible explanation is that the LM may stabilize the lumbar spine and protect the facet joints from strain during rotation.

The deep LM has a predominance of Type I slow-twitch oxidative muscle fibers (Mazis et al. 2009) and is thus well suited for long-lasting contractions. Self-sustained firing in motoneurons has been increasingly established as a mechanism behind long-lasting stable motor unit force production since its discovery 30 years ago (see review by Heckman and Enoka 2012). Descending axons from brainstem nuclei project monosynaptically to motoneurons and release monoamines that act as neuromodulators. Serotonin (5-HT) and norepinephrine facilitate the generation of positive inward currents (PICs), which change the motoneuron response to injected
current: The motoneuron amplifies the input, resulting in higher firing rates. With more intense monoaminergic stimulation the motoneuron even continues firing at a stable rate after the input has stopped. Additionally, the motoneuron becomes less sensitive to further excitatory input, a phenomenon called saturation or rate limiting. The two latter features would seem to be well suited for generation of stable long-lasting contractions during postural activity (Eken and Kiehn 1989; Eken 1998; Kiehn and Eken 1998). We have however found no previous reports exploring the existence of self-sustained firing in human back muscles.

Descending neuromodulatory projections from the brain stem to motoneurons appear to be bilateral and quite diffuse (Holstege and Kuypers 1987). Axial muscles also receive a bilateral supply from the motor cortex, and a previous study has demonstrated bilateral common drive to lumbar iliocostalis and longissimus muscles (Marsden et al. 1999). The authors concluded that common drive to axial muscles may allow the axial skeleton to act as a functional whole during postural control. Similar studies of the deepest axial back muscles do not exist.

In an attempt to improve our understanding of motor control of low back muscles and as a reference for later investigations in subjects with LBP, we implanted fine-wire EMG electrodes in healthy volunteers and studied discharge patterns of motoneurons projecting to deep LM during unhindered postural activity and during voluntary activation. In addition to the observational nature of the study, we hypothesized that individual LM MUs would be tonically active for long periods during unhindered standing and sitting. We also hypothesized that stable long-lasting tonic motoneuron activity in the LM would at least in part be caused by self-sustained discharge of motoneurons. Finally, we wanted to assess the extent of common drive to ipsi- and contralateral motoneuron pairs.
Materials and methods

Subjects

Subjects with no history of LBP, signs of neurological disease, or use of medication were recruited via electronic advertising primarily through student web sites. All subjects received detailed information prior to signing consent forms. After acceptance to the study, back function and spinal movements were assessed and demographic data including education, social status, handedness as well as exercise, smoking and coffee drinking habits were recorded. Free and full range of motion in three planes was prescriptive for inclusion as well as ability to hold the isometric back extension endurance test (Biering-Sørensen 1984) for 60 seconds (holding the unsupported upper body in a horizontal prone position with the lower body fixed) (Demoulin et al. 2006). Finger to floor distance was measured during full lumbar flexion before and after electrode implantation in order to assure that the electrode bundles did not hinder lumbar movement.

Electrodes

Flexible fine-wire electromyography (EMG) electrodes for implantation were custom made from 25 cm long, 50 µm diameter Teflon-insulated platinum/iridium wires (#776000, A–M Systems, Carlsborg, WA). In comparison the fiber diameter in human lumbar multifidus is 58–66 µm (Thorstensson and Carlson 1987). Three wires were twisted tightly together in a bundle. The distal 1–2 mm was bent back 180° creating a hook and cut transversely exposing only the three small, closely spaced recording surfaces to electrical activity in the nearby muscle fibers. Each wire was tested for conduction leaks by submerging it partly into a drop of saline and attempting to pass a 10 µA current through the fluid. All electrode bundles were sterilized prior to implantation.

Two electrode bundles were inserted under sterile conditions in all experiments, one on each side of the lumbar spine. Prior to electrode implantation, the skin was anesthetized with a small amount of lidocaine 10 mg/ml (Xylocain, AstraZeneca, London, UK) injected subcutaneously. A single-use 18G epidural needle (Portex System 1 Epidural Minipack, Smiths Medical ASD, Inc., Keene, NH) was inserted approximately 2–4 cm lateral to the L4 spinous process and directed obliquely and
medially under ultrasound guidance to reach the deepest fibers of the lumbar multifidus. The subjects often reported short-lasting pain or discomfort as the fascia surrounding the paraspinal muscles was penetrated, signifying that the small amount of subcutaneous local anesthesia had not affected deeper structures. The electrode bundle was fed all the way through the needle, and the needle was removed while slight pressure was applied to the bundle in order to avoid dislocation. To ensure minimal tissue damage only one attempt at placing the needle was allowed.

The subjects were asked to flex, extend, and rotate the back in order for the electrode bundle to settle in the tissue and to ensure it did not cause discomfort. The movements caused the electrode bundle to be drawn in through the skin by 1–4 cm before settling. After settling, the electrodes were fastened to the skin with 6 mm x 100 mm sterile reinforced adhesive skin closures (Steri-Strip R1546, 3M Health Care, St. Paul, MN), and the implantation site and electrode bundle were protected with a sterile transparent film dressing (Tegaderm Film 1626W, 3M Health Care, St. Paul, MN). After each experiment the electrode bundle was removed, measured, and checked visually to ensure that it had been removed in its entirety and that all electrode wires were undamaged.

**EMG recordings**

The fine-wire EMG electrodes were connected to amplifiers and preamplifiers (MS6 oscilloscope mainframe with AA6 Mk III and PA 63, Medelec Ltd, Woking, UK), and differential recordings were made between the two electrode wires in each bundle that provided the best possible discrimination of motor unit activity. Signals were band-pass filtered at 80 Hz to 32 kHz, monitored on a four-channel storage oscilloscope (Tektronix 5113, Tektronix Inc, Beaverton, OR) and stored on a frequency-modulation tape recorder (RTP 600B, Kyowa Electronic Instruments Co. Ltd, Tokyo, Japan) for offline analysis. Each experiment was also filmed with a digital video camera (DCR-TRV20E, Sony Corporation, Tokyo, Japan) while the analog EMG signals from both sides were fed through the microphone input. The video recordings with synchronized sound tracks were subsequently transferred to a personal computer.
Raw data was imported to a personal computer from video files, or from tape recordings using a Power1401 Mk II data acquisition interface and Spike2 software version 7 (Cambridge Electronic Design, Cambridge, UK). All analyses were performed with Spike2 software. Individual motor-unit action potentials (MUAPs) were identified and discriminated. MUAP collisions were identified and the combined MUAP was split to best match by Spike2 and confirmed or changed manually. Consecutive MUAPs were superimposed to confirm visually that they had similar waveform and thus were recorded from the same MU. The time stamp of each MUAP was stored together with unique subject and MU identifiers in a custom-built database (FileMaker Pro 11.0v3, FileMaker Inc., Santa Clara, CA) from where interspike intervals (ISIs), instantaneous discharge rates, and train lengths were calculated. MUAP trains were defined as consecutive MUAPs with interspike intervals <500 ms. Regularity of MU discharge was assessed by computing the difference between successive interspike intervals (ΔISIs), and using the inter-quartile range of the resulting distribution (ΔISI IQR) as a measure of MU discharge variability (Eken et al. 2008). MU discharge episodes with repetitive doublets were excluded from ΔISI IQR analysis.

Recording of spontaneous EMG activity during normal unhindered standing and sitting demanded that the subject be distracted from the recording process. This was accomplished by showing a comedy DVD film on a laptop computer equipped with earphones. The subjects were instructed to sit on an armless chair with hips and knees at 90 degrees and to stand erect without hand, arm, or back support. Postural adjustments were allowed in order to feel comfortable while viewing the movie. Spontaneous EMG activity was recorded without any visual or auditory feedback. Voluntary activity was recorded while the subject was standing with the spine in a slightly forward-bending position trying to recruit MUs with auditory feedback. An attempt was made to first recruit one unit into steady discharge for at least 10 seconds and then increase the load by bending further forward in order to recruit one or more additional MUs for another 10 seconds. In several cases it was not possible to follow a single-motor-unit discharge episode from beginning to end due to a gradual change in amplitude as the muscle fiber moved in relation to the electrode and drowned in background noise. Thus, gross
electrical activity in the vicinity of the electrode was used to measure total activity duration. Only high-quality recordings were used to study single MU discharge.

**Paired motor unit recordings**

In order to search for qualitative evidence of self-sustained firing in MUs, we looked in paired recordings for cases where a MU (test unit) was recruited from inactivity to its preferred discharge range or was abruptly derecruited while the discharge rate of other units which were already active (reference units) remained unchanged (Eken and Kiehn 1989; Kiehn and Eken 1997; Hornby et al. 2002).

Common drive was assessed by determining the extent of cross correlation between concurrently active units (De Luca et al. 1982; Mochizuki et al. 2006). MU discharge episodes with doublets were excluded from CDC analyses, and only activity periods lasting for at least 5 seconds were analyzed. All computations were performed off line in Spike2. A continuous waveform representing smoothed instantaneous discharge rate was calculated after spike sorting by replacing each discharge event with a 600 ms wide raised cosine waveform of unit area symmetrical about the event time. A second-order high-pass Butterworth filter with cut off frequency at 0.75 Hz was then applied to remove mean frequency and low-frequency oscillations, and cross correlograms between the high-pass filtered smoothed frequency traces from the individual MU pairs were computed. A recording could contain several activity periods, each with their individual cross correlogram. Therefore, a single resultant correlogram for each MU pair in each recording situation was computed as a weighted average of individual cross correlograms, using recording duration as weight. The common drive coefficient (CDC) was defined as the maximum value within 0±50 ms (De Luca et al. 1982) in the resultant weighted average correlogram. This procedure eliminates the inherent bias towards higher CDC values when different values are obtained from several underlying correlograms with slightly different waveforms and then averaged to obtain one common value.

**Statistical analyses**

Due to asymmetrical distributions results are given as medians with 25th and 75th percentiles unless otherwise specified. Mean discharge rates are provided for comparison with previous literature. Groups of continuous variables were compared
using the Wilcoxon–Mann–Whitney test, and linear relationships between continuous
data from a single motoneuron were investigated using simple linear regression.
Linear mixed models using the Restricted Maximum Likelihood (REML) fitting
method were utilized to test or control for the effects of a number of predefined
independent variables on median MU discharge rate, ΔISI IQR, CDC, and total EMG
activity duration. In accordance with the experimental design, spontaneous vs.
voluntary activation, sitting vs. standing, unilateral vs. bilateral MU pair (for CDC),
and median MU interspike interval (for ΔISI IQR) were always entered as
independent variables in the multivariate model that was tested. Age, sex, daily coffee
intake, whether the electrode was implanted on the side of the subject’s dominant
hand, and whether the electrode was positioned “on target” were entered provided that
the $P$ value for univariate analysis was $<0.10$. After each run, the single least
significant independent variable was removed and the model was re-run until only
variables with $P<0.05$ remained. Subject, side (left/right) nested within subject, and
MU nested within subject and side were entered as random effects to account for
repeated measures. For CDC analyses, left/right side was not part of the model, as this
would preclude analyses of unilateral vs. bilateral MU pairs. Consequently, MU pair
was only nested within subject. MU and spontaneous vs. voluntary activation were
not part of the model for total EMG activity duration.
Statistical analyses were performed using JMP 11.0.0 (SAS Institute Inc., Cary, NC).
A significance level of $P<0.05$ was assumed for all tests.

**Ethics**

All procedures were performed in accordance with the Declaration of Helsinki and
were approved by the Regional Committee for Medical Research Ethics of Southern
Norway and permitted by the Data Protection Official for Research at the Norwegian
Social Science Data Services.

**Results**

Eleven subjects (median age 25 years, range 20–40 years, 4 female) were recruited.
One male subject was excluded from the analysis due to the discovery of the use of
selective serotonin re-uptake inhibitor prescription medication not disclosed prior to acceptance in the study. One female subject was not able to complete the required tasks due to near syncope associated with phobia shortly following commencement of EMG recording. In this subject there was a marked breakdown in tonic discharge activity towards the end of the five-minute recording. One female subject had only one electrode successfully implanted. A total of 356 minutes of recordings from 17 muscles in 9 subjects (range 29–46 minutes per subject) were available for analysis (Table 1).

**Lumbar multifidus activation pattern**

In an attempt to ensure that the electrode was positioned in the target muscle, EMG activity was evaluated while each subject was asked to perform a series of movements in the standing position in which the LM is considered to be active (Morris et al. 1962; Donisch and Basmajian 1972; Valencia and Munro 1985). As expected, the greatest activation was recorded during forward flexion, extension from flexion, contralateral rotation and ipsilateral hip extension (Fig. 1). There was moderate activity during contralateral hip extension and no activity during ipsilateral rotation and standing hyperextension. Five of the 17 recordings did not show activity in all predicted movements. Four LM recordings lacked activation in contralateral rotation, one was inactive in ipsilateral hip extension, and three were inactive in contralateral hip extension. These five electrodes were classified as “not on target”. Only four muscles displayed a flexion-relaxation phenomenon (Fig. 1) with myoelectric silence in full forward flexion (Floyd and Silver 1955; Watson et al. 1997; Colloca and Hinrichs 2005). Finger to floor distance remained unchanged for all subjects and none reported pain during the experiment.

Whether the electrode was classified as “on target” or “not on target” did not influence on median MU discharge rate, ΔISI IQR, CDC or gross muscle activity duration when tested in a multivariate model (see below). We have therefore chosen to include all recordings in this report.

**Single unit discharge characteristics**

Sorting of MUs was based on their waveform as seen through the fine-wire EMG electrodes (Figs. 2 and 6). More than five hours of recording from 17 electrodes in 9
subjects was available for analysis of spontaneous motor activity (Table 1), each recording lasting 6–20 min (range) during sitting and 12–32 min during standing.

MUAPs from 33 MUs were available for analysis of activity during unhindered sitting or standing. Their median discharge rate was 5.4 pulses per second (pps) (quartiles 4.7–6.2) during sitting and 6.9 pps (6.5–7.8) during standing. Once activated, MUs continued to fire for up to several minutes with slight oscillations in discharge rate (Figs. 2, 3, and 6A). Oscillations in concurrently active MUs were in phase, and phase locked to breathing excursions. The start or end of long-lasting motoneuron discharge occasionally was seen to coincide with a deep sigh.

An additional total 15 minutes of recording rendered 48 MUs available for analysis of motor activity during voluntary standing (Table 1). Their median discharge rate was 7.4 pps (6.4–8.5). Fig. 3 shows the activity of single MUs during voluntary forward flexion while standing as the subject received auditory feedback. In addition to keeping a steady discharge rate, subjects were asked to increase the discharge rate and recruit new units by leaning forwards, and then to hold the newly recruited units at steady discharge rates. The median discharge rate of MUs at low and high voluntary effort was not significantly different (Fig. 4; \( P = 0.37 \) in a linear mixed model with subject, left/right side nested within subject, and MU nested within subject and side as random effects), and consequently the two were treated as one task in further analyses.

The distributions of median MU discharge rates in the different postural tasks are shown in Fig. 4. The contribution of variables that might influence on discharge rate in MUAP trains was evaluated in a mixed model as outlined in Methods. Any discharge rates >250 pps (i.e., intervals <4 ms) were excluded (cf. Fig. 6B), and only MUs with at least 25 interspike interval measurements were included (total 71 units with 88,683 intervals from 9 subjects). Variables for sex, coffee consumption, whether the electrode was classified as being “on target” as judged from the functional tests, and whether the unit recorded from was on the side of the dominant hand did not meet our predefined criteria for entry into the model due to their performance in the initial univariate tests. Age, spontaneous vs. voluntary activity, and sitting vs. standing were significant in univariate analyses, but the final multifactorial model demonstrated
significant effects only of sitting vs. standing with an increase of 1.72 pps from sitting to standing (95% CI 0.952–2.496; $P < 0.0001$), $R^2 = 0.61$ for the total model.

Regularity in discharge for a MU was assessed as the interquartile range for difference between successive interspike intervals ($Δ$ISI IQR; Table 1). Evaluated with the same mixed model approach, $Δ$ISI IQR for individual MUs increased with their median interspike interval duration as expected (Matthews 1996) (1.15 ms $Δ$ISI IQR increase per ms increase in median interspike interval; CI 0.65–1.64; $P < 0.0001$), as well as with standing (53.57 ms increase vs. sitting; 95% CI 10.67–96.47; $P = 0.015$), $R^2 = 0.13$ for the total model.

**Doublets**

For analysis purposes, doublets were defined as two action potentials of the same shape and nearly the same amplitude, occurring consistently in the same relation to one another at an interval of 2.5–20 ms (Simpson 2002).

Doublets would occur as one or a few at the very beginning of discharge episodes, or as periods of discharge lasting up to tens of seconds during tonic activity. Fig. 5 shows initial doublets and Fig. 6A sustained doublet discharge, both during spontaneous standing. The distribution of inter-spike intervals from the unit producing doublets in Fig. 6A is shown in Fig. 6B. Median intra-doublet interval duration was 5.55 ms (quartiles 5.25–6.02 ms; shortest interval 4.56 ms; n = 1714), whereas median interval duration during non-doublet activity was 124 ms (quartiles 106–146; n = 964). The interval following a doublet was significantly longer than interspike intervals during non-doublet activity (median inter-doublet interval 205 ms (176–245); n = 1540; post-doublet interval before single spike 196 ms (160–243); n = 63; pre-doublet interval after single spike 171 ms (146–210); n = 74; $P < 0.0001$ vs. interspike intervals during non-doublet discharge for all). The relationship between two ensuing interspike intervals is explored further in Fig. 6C. The discharge rates of two neighboring non-doublet intervals are highly correlated (lower part of scatterplot in Fig. 6C), and a high-rate doublet almost only follows lower-rate intervals (upper part of the scatterplot).
**Common drive and rotation of activity**

Examples of data from simultaneous recordings of two and three spontaneously active units from different subjects are shown in Figs. 6A and 2 respectively. The concurrently active units modulated their discharge rates in synchrony, indicative of a common drive. However, they started and ended their MUAP trains seemingly independent of one another, usually by abrupt changes between inactivity and long-lasting stable discharge at approximately 7 pps, while other simultaneously active units showed little or no change in their discharge rate. Figs. 6A and 2 also show rotation of activity between units, here defined as occurring when a MU (test unit) was recruited from inactivity to stable tonic discharge while another MU (reference unit) continued to fire with little or no change in discharge rate, and the reference unit subsequently was derecruited while the more recently recruited test unit continued to fire with little or no change in discharge rate. Stable discharge persisted for up to several minutes, however in many instances movement artifacts and gradual changes in MUAP shape or amplitude made it difficult or impossible to follow units from recruitment to derecruitment.

Quantitative assessment of common drive was performed using common drive coefficient (CDC) analysis in 44 unilateral and 43 bilateral unit pairs (Table 1; Figs. 3 and 7) from 9 subjects (median 9 pairs per subject; range 1–17 pairs). High CDC values indicate that MUs receive a strong common drive (De Luca et al. 1982; De Luca and Erim 1994). The final multivariate model demonstrated significant effects of bilateral vs. unilateral unit pairs (CDC for bilateral pairs decreased by 0.086 relative to unilateral; 95% CI 0.002 to 0.170; \( P = 0.045 \)), and spontaneous vs. voluntary (CDC for spontaneous activity increased by 0.217 relative to voluntary; 95% CI 0.102 to 0.332; \( P = 0.0004 \)), \( R^2 = 0.92 \) for the total model. The CDC values for unilateral and bilateral MU pairs during spontaneous standing were remarkably similar (Table 1; cf. Figs. 7A and B), and we found no significant difference when they were tested in the multivariate model (\( P = 0.88 \); 23 MU pairs in 5 subjects). For spontaneous sitting, we considered the material too small to draw any meaningful conclusions (7 MU pairs in 3 subjects). Median absolute time lag from zero for the total population of MU pairs was 0.044 s (quartiles 0.013–0.050); mean time lag was 0.034 s (95% CI 0.030–0.038).
Gross muscle activity

A crude estimate of the duration of episodes of spontaneous gross muscle activity was obtained by measuring gross EMG activity picked up by the fine-wire EMG electrodes (Table 1), and potential contribution to total activity duration was tested for sex, age, coffee consumption, whether the recording was from the side of the dominant hand, and whether the electrode was classified as being “on target”. None of the variables contributed significantly in univariate analyses, and thus they were not tested in a multivariate regression model.

Discussion

The present study of motor activity in the deep LM during postural tasks confirms that the LM is active as an anti-gravity muscle and in ipsilateral rotation. No effect was found on total duration of gross muscle activity for the variables that were tested, but significant effects of sitting vs. standing were seen on median discharge rate and interspike interval variability in LM MUs. Several LM units fired doublets. The discharge rates of simultaneously active MUs were modulated in phase, and phase locked to breathing excursions. Common drive coefficient analysis demonstrated significantly lower CDC values in bilateral MU pairs compared to unilateral pairs for the total material, but surprisingly there was no significant difference during spontaneous standing. Median CDC values for spontaneous standing were also higher than for spontaneous sitting and voluntary standing. In spite of common drive, motoneurons were recruited from inactivity to tonic discharge lasting for several minutes without changes in discharge rate in already active units, and several instances were documented where activity was rotated between MUs. We argue that this behavior is indicative of self-sustained discharge in LM motoneurons, and suggest that intrinsic motoneuron properties constitute a central mechanism for postural control of deep back muscles.

Activity in movements

Although our movement testing protocol was only designed to verify that the electrodes were positioned in the correct muscle, some of our observations should be mentioned: We confirmed that the deep LM was active in extension against resistance
and in contralateral rotation, particularly at peak rotation position. We also found that it was active in full forward flexion when the subjects were not specifically asked to relax, indicating a similar active role throughout the full flexion range. This suggests that the multifidus protects the spine by actively restricting lumbar end range of motion both in flexion and rotation.

**Discharge rate**

The median discharge rates of motoneurons to deep LM in the present material were well within the typical range reported for repetitive discharge in human MUs (Duchateau and Enoka 2011) and close to mean discharge rates found in lumbar iliocostalis and longissimus muscles (6.3–6.7 pps; Marsden et al. 1999). Median MU discharge rate was significantly lower during spontaneous sitting (5.4 pps) than during spontaneous standing (6.9 pps), but did not differ significantly between spontaneous and voluntary tasks. The effect of this difference in discharge rate on contractile force is difficult to assess, since the tension–frequency relationship for human multifidus muscle is unknown.

Recruitment of MUs to tonic discharge during unhindered posture often occurred abruptly from no activity to a discharge rate range that was subsequently maintained for up to several minutes (Figs. 2 and 6). Similarly, when subjects producing low-level voluntary force were asked to increase force production, more units were recruited but already active units maintained their discharge rate (Fig. 4). No solid conclusions can be drawn from the latter observations, since generated force was not measured and the range of forces was probably limited. There may also have been complex changes in motor unit recruitment threshold and order due to shifts between tasks, e.g. isometric, shortening, and lengthening contractions, that could not be controlled for in our experiments (Enoka and Fuglevand 2001). However, we find it tempting to speculate that the observed phenomena might be caused by activation of persistent inward currents (PICs; cf. discussion of self-sustained discharge below) in the motoneurons. Amplification of synaptic drive followed by sharp limitation of the efficacy of additional synaptic input is a fundamental property of PICs, underlying the initial steep increase in firing rate and subsequent “rate limiting” or the “preferred firing range” that can be seen in motoneurons (Heckman et al. 2008). A consequence
of this is that increased force production primarily occurs due to recruitment of more MUs.

**Doublets**

Particularly short interspike intervals (doublets) inserted early in a MUAP train may have remarkable functional consequences, as they can lead to faster buildup of muscle force as well as to a maintained higher level of force production (Burke et al. 1970). High-rate doublet discharges have been reported in a large number of human muscles (Garland and Griffin 1999). In the present material, several examples were found where a motoneuron generated pairs of action potentials with particularly short intervals, typically around 5–6 ms. These high-rate doublets occurred at the start of action potential trains, or when motoneurons were discharging tonically at low rates. The properties of the high-rate doublets in the present study correspond to those described by Bawa and Calancie (1983), who list the following criteria for identification: Intradoublet interval generally less than 10 ms; the second spike in a doublet of similar shape and amplitude always less than or equal to that of the first spike; and always followed by a longer interval than those occurring during single discharges. Further, the distribution of intra-doublet intervals in Fig. 6B bears a striking resemblance to that in their Fig. 2, even though their intervals for single discharges are markedly shorter than those in the present study.

High-rate doublets are assumed to arise from a delayed depolarization, often referred to as a post-spike hump, during the falling phase of the action potential (Bawa and Calancie 1983; Garland and Griffin 1999). Fig. 6 illustrates a period with a high amount of doublets in one of two motor units that were modulated in parallel indicative of a strong common drive. The lower part of Fig. 6C shows that the discharge rates of two neighboring non-doublet intervals were highly correlated, and that high-rate doublets (upper part of the scatterplot) almost only occurred after low-rate intervals. This could conceivably be caused by prolonged post-doublet intervals during repetitive doublet activity, or conversely be due to doublets preferably occurring during low-level drive to the motoneuron. We argue that low-level drive is the probable determinant for the doublet discharges in Fig. 6, since doublets seemed to occur primarily when the other motor unit was discharging at slightly lower rates (Fig. 6A).
In contrast to high-rate doublets, short initial interspike intervals in ballistic movements probably occur due to massive synaptic input (Bawa and Calancie 1983). The initial short interspike intervals in Fig. 5 that occurred when the subject made slight postural adjustments probably belong to this class. They are mostly within the 5–15 ms interval range reported by Thomas et al (1999) to produce the greatest forces and force-time integrals in human thenar motor units. In their study, such initial doublets caused force to increase to mean 3.5 times the force of single twitches, corresponding to an average 48% of maximum tetanic force and an average force-time integral 5.6 times that of the initial twitch. The authors found maximum force-time integrals when motor units were stimulated at approximately 7 pps after the initial doublet, i.e. that doublets would make thenar muscles contract with maximum efficiency even when the motor units are activated at their minimum rates. Consequently, the functional role of the initial doublets in Fig. 5 could be to ensure rapid onset of force in order to stabilize the spine when the center of gravity moves forward. In contrast to initial doublets, short intervals inside trains may only lead to small and short-lasting changes in force (Duchateau and Enoka 2011), and their functional role remains unclear.

**Common drive**

The most conspicuous expressions of common drive are the relatively large respiratory-related fluctuations in discharge rate that can be seen in Fig. 3. Respiratory-motor interactions have been demonstrated in humans both for automatic and voluntary breathing (see (Li and Rymer 2011)) as well as in animals, e.g. rat soleus muscle (Eken 1998). Synchronous fluctuations in MU discharge rate still remain in smoothed discharge rate curves after the respiratory-related fluctuations have been removed by high-pass filtering (Fig. 3). Common drive coefficients are calculated from cross correlograms between pairs of such curves. Common drive coefficients for MU pairs were significantly higher during spontaneous than during voluntary force production. This is in line with results from the soleus muscle, where Mochizuki et al. (2006) reported significantly higher CDC values during postural tasks than during voluntary isometric tasks. Thus, it seems that control strategies for spontaneous and voluntary contractions differ also in axial muscles. Further, CDC values in unilateral MU pairs have previously been shown to
be significantly higher than in bilaterally recorded motor unit pairs, both in the soleus muscle during spontaneous standing and voluntary contractions while sitting (Mochizuki et al. 2006) and in weak voluntary contractions in lumbar paraspinal muscles during sitting (Marsden et al. 1999). This was also the case in the present material although interestingly not during spontaneous standing. The number of units in the different materials are comparable, with 44 unilateral and 43 bilateral pairs in the present study, 57 unilateral and 14 bilateral lumbar paraspinal pairs in the study by Marsden et al. (1999), and 36 unilateral and 67 bilateral soleus pairs published by Mochizuki et al. (2006). The equally strong bilateral common drive during spontaneous standing in our material points to the unique role of the bilateral axial back muscles in working as a functional unit to extend and stabilize the spine while in an upright position. The anatomical substrate is probably the particularly high degree of bilateral descending projections to motoneurons to axial muscles (see Marsden et al. 1999).

Self-sustained discharge and rotation of active motor units

In spite of pronounced uni- and bilateral common drive, motoneurons were recruited abruptly from inactivity with no or only minor change in the discharge rate of already active units (Figs. 2 and 6A). We argue that this behavior may be indicative of self-sustained discharge due to activation of PICs in LM motoneurons (Eken and Kiehn 1989; Kiehn and Eken 1997; Eken 1998; Hornby et al. 2002), adding to the above arguments for the existence of PICs based on abrupt recruitment and subsequent narrow discharge rate range. To our knowledge this is the first report to discuss a possible contribution from intrinsic motoneuronal properties to postural control of deep back muscles.

We also demonstrate spontaneously occurring rotation between MUs (Figs. 2 and 6A). The definition of rotation is merely incremental, requiring in addition to the above criteria for self-sustained discharge that a MU was derecruited while a more recently recruited MU continued to fire with little or no change in discharge rate. Rotation of MU activity has been proposed as a mechanism that protects postural muscles from excessive fatigue during sustained contractions (Westgaard and de Luca 1999; Jensen et al. 2000), and as beneficial in maintaining a constant force production whilst allowing the contractive elements of the silent MUs to recover their ability to generate
force (Forbes 1922; Bawa et al. 2006; Bawa and Murnaghan 2009). Rotation of
activity also allows for distributed endurance training of the muscle fibers and has
been suggested to be responsible for the maintenance of homogeneous slow muscle-
fiber properties in postural leg muscles (Eken 1998).

Self-sustained discharge in motoneurons is dependent on descending monoaminergic
input from the brainstem, particularly serotonergic and noradrenergic systems
(Heckman et al. 2008). Interestingly, serotonin has been found to activate both
facilitatory 5-HT\textsubscript{2} receptors in the dendrites as well as inhibitory 5-HT\textsubscript{1A} receptors at
the axon initial segment creating a cellular mechanism for inducing central fatigue by
serotonin spillover from the raphe-spinal pathway (Cotel et al. 2013), and thus a
possible mechanism for both inducing and quenching long-lasting discharge in
motoneurons, and thereby also for rotation of activity among them. However, the
underlying mechanism for rotation of activity between motoneurons in the present
material can obviously not be determined.

Limitations

The observational character of the study is a clear limitation, as is the lack of previous
data from LM, and the reported findings should only be regarded as hypothesis
generating. Any inference from motor unit activity to function is also speculative until
properly tested. However, we hope that our findings may alleviate the scarcity of
single-unit EMG data from deep paraspinal muscles and constitute a starting point for
later experiments with formal hypothesis testing.

We cannot be certain that pain associated with indwelling electrode wires or the
implantation procedure did not affect the experimental situation. However, the
participants reported no pain during the experiment, and their range of movement did
not seem to be limited in any way. There is some evidence that insertion of fine-wire
electrodes does not alter EMG patterns in normal adults (Jacobson et al. 1995).

Ultrasound guidance was not ideal during electrode implantation due to profound
bone shadows. It was also not possible to visualize the electrode in its entirety, and
confirmation of correct position was consequently not possible. We can therefore not
be absolutely certain that we have measured from the target area in all experiments.
CT may be a better tool in this respect, in particular when exact positioning is
mandatory due to the complex overlapping of muscle fascicles lateral to the target segment that makes a specific segment extremely difficult to isolate. However, we do not think that we have made systematic placement errors.

There was no endeavor to control for posture type in our subjects, although it would be reasonable to consider different posture strategies producing different EMG patterns. We recommend thorough documentation of such strategies, preferably also video filming the subjects from different angles.

Lastly, it was often difficult to discriminate and follow individual MUs from the beginning to the end of prolonged discharge episodes. Amplitude and shape of MUAPs tended to change, and to blend with those of newly recruited MUs. As a consequence, we do not report statistics for duration of discharge, which would clearly have been of great interest. However, the findings we report are only those that are based on high quality data.

**Conclusion**

The role of the lumbar multifidus as a postural muscle in the upright human requires the ability to generate bilateral long-lasting stable motor unit force production without fatigue. We have demonstrated that although under influence of bilateral common drive, long-lasting activity within narrow firing rate ranges was rotated between motor units, and we suggest that this was probably due to activation and inactivation of self-sustained discharge in the motoneurons, allowing distribution of activity and rest between muscle fibers over time. Common drive analysis showed that different strategies were in play when attempting to keep a fixed force output as opposed to when force was kept constant unconsciously. It is apparent from rat studies that evidence for rotation of activity between MUs is not seen until one studies spontaneous motor behavior during everyday life (Eken and Kiehn 1989). There are reasons to believe that this is true in humans as well (Kiehn 1991).

To our knowledge this is the first study to observe spontaneously occurring tonic activity in motoneurons to human postural back musculature. It is our hope that the present study will constitute a reference material for further research into the normal physiology of posture and possible changes due to low back pain.
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Disclosures

No conflicts of interest, financial or otherwise, are declared by the authors.
References


Enoka RM, Fuglevand AJ. Motor unit physiology: some unresolved issues. *Muscle
Floyd WF, Silver PH. The function of the erectors spinae muscles in certain

Forbes A. The interpretation of spinal reflexes in terms of present knowledge of

Garland SJ, Griffin L. Motor unit double discharges: statistical anomaly or


Heckman CJ, Johnson M, Mottram C, Schuster J. Persistent inward currents in
spinal motoneurons and their influence on human motoneuron firing patterns.

Holstege JCJ, Kuypers HGH. Brainstem projections to spinal motoneurons: an

Hornby TG, McDonagh JC, Reinking RM, Stuart DG. Motoneurons: A preferred

Jacobson WC, Gabel RH, Brand RA. Insertion of fine-wire electrodes does not

Jensen BR, Pilegaard M, Sjøgaard G. Motor unit recruitment and rate coding in
response to fatiguing shoulder abductions and subsequent recovery. Eur J Appl

Kiehn O, Eken T. Prolonged firing in motor units: evidence of plateau potentials in


Kiehn O. Plateau potentials and active integration in the “final common pathway” for

Li S, Rymer WZ. Voluntary breathing influences corticospinal excitability of

Macintosh JE, Valencia F, Bogduk N, Munro RR. The morphology of the human

Maniadakis N, Gray A. The economic burden of back pain in the UK. Pain 84: 95–

and bilateral control of motor unit pairs in the first dorsal interosseous and paraspinal


**Figure captions**

Fig. 1. Bilateral raw fine-wire electromyography signals from deep lumbar multifidus (LM) during voluntary activation whilst standing. Instructions for movements are indicated below. The deep LM was eccentrically active in forward flexion and concentrically active in extension from flexion bilaterally, and unilaterally active in contralateral rotation and in ipsilateral hip extension. Additionally, in this subject, the right LM was active during contralateral hip extension. The flexion-relaxation phenomenon, where the LM was not active during full flexion (Floyd and Silver 1955; Watson et al. 1997; Colloca and Hinrichs 2005) is evident.

Fig. 2. Unilateral recording showing concurrently active motor units (MUs) during 7 minutes of spontaneous standing (same subject as in Fig. 5). From bottom to top: Unprocessed analog signal (black), discriminated motor unit action potentials (MUAPs) (color coded), superimposed smoothed discharge rates, and instantaneous discharge rates for individual units. Insets in the three upper traces show superimposed consecutive MUAPs acquired over 10 second periods. The middle (blue) MUAPs remain similar in shape in spite of changes in amplitude. Changes in MUAP amplitude were interpreted to be caused by movements of the muscle fiber relative to the electrodes, and often limited the duration of time periods where unequivocal MUAP sorting was possible. Note the synchrony in discharge rate fluctuations between concurrently active MUs indicating a common drive. In spite of this, there is rotation of activity among the MUs, probably reflecting activation and deactivation of self-sustained discharge in the individual motoneurons.

Fig. 3. Bilateral recordings showing five concurrently active MUs (color coded) under voluntary forward flexion with auditory and visual feedback (same subject as in Fig. 6). A second-order high-pass Butterworth filter with cutoff frequency 0.75 Hz was applied to the smoothed discharge rate traces to remove mean frequency and low-frequency oscillations (upper traces both sides) before common drive coefficient (CDC) analysis. Oscillations remain correlated (dashed lines) within and between sides even after removal of the larger respiratory related fluctuations seen in the single-unit instantaneous discharge rate traces, indicating a strong bilateral common drive.
Fig. 4. Distribution of median MU discharge rates for spontaneous activity during sitting, and for spontaneous and voluntary activity during standing. Boxes show medians and quartiles; whiskers denote 10 and 90 percentiles. Standing contributed significantly toward higher median discharge rates (see Table 1).

Fig. 5. Unilateral recording from a single deep LM MU of a healthy, physically fit subject (same subject as in Fig. 2) during spontaneous standing. Slight changes in posture and breathing turned on and off MUAP trains all starting with two or three doublets with long post doublet intervals (inset).

Fig. 6. Unilateral recording from the deep LM during spontaneous standing, same subject as in Fig. 3. A: From bottom to top: Unprocessed analog signal (black), discriminated MUAPs (color coded), superimposed smoothed discharge rates, and instantaneous discharge rates for individual units. The upper trace shows repetitive doublet discharges occurring at low discharge rates. Insets show superimposed MUAPs during 10 s doublet discharge and 10 s non-doublet discharge. Note rotation of activity between the MUs. B: Interspike interval histogram obtained during sustained doublet discharge. Note different time scales. C: Poincaré plot showing the relationship between 1977 non-doublet interspike intervals (defined as interspike interval >20 ms) and their immediately following interspike intervals. Note that high-rate doublets are consistently preceded by low-rate intervals, and that the intradoublet instantaneous rate becomes lower as the instantaneous rate of the preceding interval increases (separate regression lines with 95% CI for intervals followed by doublets and non-doublets).

Fig. 7. A: Distribution of common drive coefficients (CDCs) in 87 motor unit pairs with median recording duration of 30.5 s (range 5.7–1044 s). Spontaneous activity contributed significantly toward higher CDCs (see Table 1). B: Cross correlograms from unilateral and bilateral recordings of MU pairs during spontaneous standing (cf. corresponding CDC values in A). CDC was defined as the maximum value within 0±50 ms (hatched vertical lines).
Fig. 1

Right multifidus

Left multifidus

Rotation right
Rotation left

Extension
Flexion

Torso

Torso

Right hip
Left hip
Fig. 2
Fig. 3

Time (s)

Right

Discharge rate (pps)

Left

Discharge rate (pps)
Median discharge rate (pps)

Spontaneous
Sitting
Standing
Voluntary
Low effort
High effort
Voluntary

Fig. 4
### Table 1. Statistics, grouped data

<table>
<thead>
<tr>
<th>Subjects</th>
<th>Total</th>
<th>Spontaneous sitting</th>
<th>Spontaneous standing</th>
<th>Voluntary standing</th>
</tr>
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<tbody>
<tr>
<td>Number (m:f)</td>
<td>9 (6:3)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age (years) (median; range)</td>
<td>25 (20–40)</td>
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<tr>
<td>Dominant side (right:left)</td>
<td>8:1</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Coffee consumption (cups/day) (median; range)</td>
<td>1 (0–4)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Electodes recorded from (on target : off target)</td>
<td>17 (13:4)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Recording time (minutes) (sum; range)</td>
<td>356 (29–46)</td>
<td>147 (6–20)</td>
<td>195 (12–32)</td>
<td>15 (1–4)</td>
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</table>

#### Gross muscle activity

<table>
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<tr>
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<th>Spontaneous sitting</th>
<th>Spontaneous standing</th>
<th>Voluntary standing</th>
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<tr>
<td>Gross activity recordings, subjects and sides, total material (n)</td>
<td>17</td>
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<td></td>
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<tr>
<td>Duration of gross activity, subjects and sides, total material (min)</td>
<td>214</td>
<td></td>
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<tr>
<td>Duration of gross activity, per subject and side (s) (median; range)</td>
<td>16 (0–1116)</td>
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<td>Duration of gross activity, per subject and side (% of recording time; range)</td>
<td>2 (0–98)</td>
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#### Single-unit activity within spike trains*

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<th>Voluntary standing</th>
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</thead>
<tbody>
<tr>
<td>Units, total material (n) (on target : off target)†</td>
<td>71 (53:18)</td>
<td>9 (6:3)</td>
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<tr>
<td>Duration of analyzed single-unit activity, total material (minutes)</td>
<td>226</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Duration of analyzed single-unit activity, per unit (s)</td>
<td>226 (33–591)</td>
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<tr>
<td>Duration of analyzed single-unit activity, per unit (% of recording time)</td>
<td>20 (4–55)</td>
<td></td>
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</tbody>
</table>

#### Intervals, total material (n) | 88683 | 14928 | 55355 | 18400
#### Intervals, per unit (n) | 1328 (143–3193) | 1541 (382–3078) | 324 (148–563) |
| Median discharge rate, per unit (pps) | 5.35 (4.66–6.19) | 6.86 (6.46–7.77) |
| Mean discharge rate, per unit (pps) | 5.40 (4.67–6.40) | 7.25 (6.70–8.89) |

#### Coefficient of variation for interspike intervals, per unit (%)

<table>
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<tr>
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<th>Spontaneous standing</th>
<th>Voluntary standing</th>
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<td>Intervals, per unit (n)</td>
<td>1328 (143–3193)</td>
<td>1541 (382–3078)</td>
<td>324 (148–563)</td>
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</tr>
<tr>
<td>Median discharge rate, per unit (pps)</td>
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<td>6.86 (6.46–7.77)</td>
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</tr>
<tr>
<td>Mean discharge rate, per unit (pps)</td>
<td>5.40 (4.67–6.40)</td>
<td>7.25 (6.70–8.89)</td>
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#### Common drive coefficients

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<th>Spontaneous standing</th>
<th>Voluntary standing</th>
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</thead>
<tbody>
<tr>
<td>Unit pairs, unilateral (n)‡</td>
<td>44</td>
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<tr>
<td>Unit pairs, bilateral (n)</td>
<td>43</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>CDC, unilateral</td>
<td>0.22 (0.04–0.40)</td>
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<td></td>
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<tr>
<td>CDC, bilateral</td>
<td>0.34 (0.14–0.58)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>CDC, bilateral</td>
<td>0.22 (0.04–0.40)</td>
<td></td>
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</tbody>
</table>

Numbers are medians and quartiles unless otherwise specified

* Spike trains are defined as consecutive spikes with intervals <500 ms. All analyses of firing frequencies and ∆ISI IQR are in trains with ≥25 intervals; discharge rates higher than 250 pulses per second (pps) are excluded.

† 11 units were recorded from in more than one task: One in spontaneous sitting and spontaneous standing; 8 in spontaneous standing and voluntary standing; 2 in voluntary standing and spontaneous sitting. No unit was recorded from in more than two tasks.

‡ 1 unit pair was recorded from in both spontaneous and voluntary standing.