RESEARCH ARTICLE

Oscillations in motor unit discharge are reflected in the low-frequency component of rectified surface EMG and the rate of change in force

Yasuhide Yoshitake · Minoru Shinohara

Abstract Common drive to a motor unit (MU) pool manifests as low-frequency oscillations in MU discharge rate, producing fluctuations in muscle force. The aim of the study was to examine the temporal correlation between instantaneous MU discharge rate and rectified EMG in low frequencies. Additionally, we attempted to examine whether there is a temporal correlation between the low-frequency oscillations in MU discharge rate and the first derivative of force (dF/dt). Healthy young subjects produced steady submaximal force with their right finger as a single task or while maintaining a pinch-grip force with the left hand as a dual task. Surface EMG and fine-wire MU potentials were recorded from the first dorsal interosseous muscle in the right hand. Surface EMG was band-pass filtered (5–1,000 Hz) and full-wave rectified. Rectified surface EMG and the instantaneous discharge rate of MUs were smoothed by a Hann-window of 400 ms duration (equivalent to 2 Hz low-pass filtering). In each of the identified MUs, the smoothed MU discharge rate was positively correlated with the rectified-and-smoothed EMG as confirmed by the distinct peak in cross-correlation function with greater values in the dual task compared with the single task. Additionally, the smoothed MU discharge rate was temporally correlated with dF/dt more than with force and with rectified-and-smoothed EMG. The results indicated that the low-frequency component of rectified surface EMG and the first derivative of force provide temporal information on the low-frequency oscillations in the MU discharge rate.

Keywords Common drive · Cross-correlation · dF/dt

Introduction

Fluctuations in muscle force during steady voluntary contraction are associated with the degraded functional ability of an individual to control voluntary movement, ranging from hand to whole body control (Kornatz et al. 2005; Kouzaki and Shinohara 2010). Fluctuations in muscle force are often increased with various factors and conditions such as divided attention, stress, inactivity, and aging (Enoka et al. 2003; Shinohara et al. 2003; Christou et al. 2004; Yoshitake et al. 2007; Johnson and Shinohara 2012). Accordingly, mechanistic investigations into the characterization of force fluctuations and their contributors, such as neural activity patterns, are valuable for understanding motor control in healthy and clinical populations. Force fluctuations during steady voluntary contractions are mainly composed of low-frequency oscillations (<5 Hz, peak power around 2 Hz) (Taylor et al. 2003; Yoshitake et al. 2004, 2008; Yoshitake and Shinohara 2013). A simulation study has suggested that the low-frequency force fluctuations are, at least in part, due to the discharge rate variability of a pool of motor units (MUs) around 1 Hz (Taylor et al. 2003). Experimental studies have also demonstrated that the temporal characteristics of force fluctuations at 1–2 Hz are correlated with the oscillations of the instantaneous MU discharge rate at low

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frequency, termed common drive (De Luca et al. 1982; De Luca 1985). Hence, the low-frequency oscillations in MU activity contribute to force fluctuations during steady contractions (Laidlaw et al. 2000; Taylor et al. 2003; Kornatz et al. 2005). Therefore, detection of MU discharges from intramuscular EMG is an essential procedure to understand the neural mechanisms for fine motor control.

Detection of MU discharges, however, usually requires invasive procedures using indwelling electrodes. It also has limitations in the range of contraction intensity, number of samples, and number of muscles with detectable MUs and thus represents only a limited portion of MU pools. In contrast, interference electromyogram using surface electrodes (surface EMG) is noninvasive and less uncomfortable to measure. Additionally, surface EMG includes a summed neural signal reflecting the number of recruited MUs and their discharge rate. Therefore, surface EMG may be more feasible and useful for understanding the neural oscillations of a pool of MUs during voluntary contractions. For studying oscillations in the activity of MU pool via surface EMG signals, a prevailing method of full-wave rectification has been employed (Mima and Hallett 1999; Myers et al. 2003; Yao et al. 2007). While oscillations in force and instantaneous MU discharge rate are mainly <5 Hz, previous research has focused on the oscillations in rectified EMG ≥6 Hz (Conway et al. 1995; Baker et al. 1997; Brown 2000; McAuley and Marsden 2000; Johnson et al. 2011), neglecting the lower-frequency oscillations in rectified EMG.

We recently demonstrated that rectified surface EMG at low frequencies (<5 Hz) was temporally correlated with force fluctuations during steady voluntary contraction in the first dorsal interosseus muscle (Yoshitake and Shinohara 2013). It has also been demonstrated that force fluctuations during steady voluntary contractions are temporally correlated with the low-frequency oscillations in the instantaneous MU discharge rate at 1–2 Hz (De Luca and Mambrito 1987; Negro and Farina 2012). Since low-frequency neural input spans across a large pool of motor units (De Luca et al. 1982), oscillations in the discharge rate of single MUs may be observable in rectified surface EMG at low frequencies, especially at low contraction intensity because the relative contribution of a single MU to surface EMG signal decreases with increases in contraction intensity. Taken together, it was hypothesized that the low-frequency component of rectified surface EMG would be temporally correlated with low-frequency oscillations in the instantaneous MU discharge rate when tested at low contraction intensity. Note that it is not readily predictable whether or not there is a temporal relation between low-frequency oscillations in MU discharge rate and low-frequency component of rectified EMG for the following reasons. The two signals are distinct in that surface EMG is continuous time-series waveforms made of action and resting potentials from a pool of MUs, whereas the signal used for assessing oscillations in MU discharge rate is discrete information on the intervals of action potentials. In addition, the low-frequency component of surface "unrectified" EMG is removed in the standard high-pass filtering procedure at ~5–20 Hz during the recording or post-processing (e.g., Negro et al. 2009; Yoshitake and Shinohara 2013), thus removing the frequencies of interest in this study. Furthermore, rectification of surface EMG alters its frequency characteristics nonlinearly (Farina et al. 2004). Accordingly, the assessment of temporal correlation between the low-frequency component of rectified surface EMG and low-frequency oscillations in the instantaneous MU discharge rate is novel and important.

In our previous study, we also found that rectified surface EMG at low frequencies recorded during steady contractions was temporally correlated with the rate of change in force (first derivative of force: dF/dt) and that the degree of this temporal correlation was greater compared with that between rectified surface EMG and force itself (Yoshitake and Shinohara 2013). Accordingly, it was also hypothesized that the low-frequency oscillations in the instantaneous MU discharge rate would be temporally correlated with dF/dt, and the correlation would be higher than that with force. Hence, the second purpose of this study was to test whether low-frequency oscillations in the instantaneous MU discharge rate are temporally correlated with the rate of change in force (i.e., dF/dt) as well as force itself.

For these purposes, the MU discharge rate, surface EMG signal, and force signal were examined during steady voluntary contraction with the first dorsal interosseus muscle, a relatively simple and well-studied human experimental model. To further examine whether the possible temporal correlations between the above-mentioned signals are sensitive in reflecting the magnitude changes in the low-frequency oscillations, the current study employed single and dual tasks for varying the amount of fluctuations in motor output.

Methods

Data were obtained from 9 healthy young adults (7 men and 2 women; 22.4 ± 1.4 years: mean ± SD; range: 21–24 years). All subjects reported an absence of current or medical history of neuromuscular disorder and were right-hand dominant. They gave written informed consent according to the procedures approved by the ethics committee of the National Institute of Fitness and Sports in Kanoya.

Experimental arrangement

Subjects performed submaximal unilateral (single) and bilateral (dual) tasks with their hands. In the single task,

steady-force isometric contractions were performed with the first dorsal interosseus muscle of the right hand only. The orientation of the right arm and hand was similar to that of our previous studies (Yoshitake et al. 2008; Yoshitake and Shinohara 2013). The right shoulder was abducted ~45°, the elbow joint was flexed to a right angle, and the wrist was fully pronated. The right arm was fixed with a vacuum foam pad. The right index finger was fully extended in the horizontal plane and the thumb was extended in a horizontal position and held with a brace. The index finger was placed in a splint that was positioned on the lateral surface of the index finger around the proximal interphalangeal joint and was connected to a force transducer. The other three fingers were flexed around a semicircular grip and fixed by a strap.

In the dual task, steady pinch-grip force was exerted by the left hand simultaneously with abduction force production by the right hand as described above. With the left forearm and hand placed on their left thigh in a comfortable position, subjects used the thumb and index finger of their left hand to exert pinch-grip force. We have employed the pinch-grip force to form a dual task with the expectation of augmenting the fluctuations in motor output in the right hand due to divided attention.

For visual guidance of exerted force, a 21-inch computer monitor was positioned at eye level to the subjects at a distance of 1.0 m. The abduction force in the right hand and the pinch-grip force in the left hand were simultaneously displayed in real-time as dots on the monitor with the X–Y mode, plotting the force of the right hand against that of the left hand (0 during the single motor task).

Maximal voluntary contraction (MVC)

Before the performance of the submaximal tasks, subjects performed a unilateral MVC task in each hand—index finger abduction in the right hand and pinch grip in the left hand. The MVC involved a gradual increase in force exerted from baseline to maximum in 3–4 s and then sustained at maximum for approximately 2 s with visual feedback. The timing of the task was based on a verbal count given at 1-s intervals, with vigorous encouragement from the investigators when the force began to plateau. Subjects performed at least three MVC trials for each hand, with subsequent trials performed if the differences in the peak force of two MVCs were >5 %. There was a rest period of at least 1 min in between trials and trials were randomized between hands. Subjects were allowed to reject any attempts which they considered not to be their maximal effort. The greatest peak force of all trials was determined as MVC force for each hand.

Submaximal single and dual tasks

After MVC following the insertion of a wire electrode into the right hand, submaximal tasks were performed. Subjects slowly increased the abduction force in the right hand to approximately 40 % MVC over 10 s to identify unique MU discharges to be recorded and to determine the recruitment threshold of the MU. The recruitment threshold of an identified MU was determined as the lowest force at which the MU started discharging action potentials tonically. Once clear single MU action potentials were identified, a target force was set at 20 % above the recruitment threshold. The exerted force and target force were represented as two dots on the monitor. In the single task, subjects were asked to match the index finger abduction force in the right hand with the target force as steadily as possible while keeping the left hand relaxed. In the dual task, subjects were asked to concurrently produce pinch-grip force with their left hand at the same relative contraction intensity as the right hand, also as steadily as possible. Contraction duration in each trial was 18 s. A practice trial was performed for several seconds before the data collection. There was a rest period of at least 1 min between trials.

Data recording and analysis

For the mechanical signals, the abduction force of the right index finger and the pinch-grip force of the left hand were measured with strain gauge transducers (LUR-A-100NSA1, 3.5 cm wide, Kyowa Electronic Instruments, Tokyo, Japan; 0.19 V/N). These forces were amplified and low-pass filtered (<100 Hz) with DC amplifiers (DPM 700, Kyowa Electronic Instruments, Tokyo, Japan).

For the neural signals, surface EMG and MU action potentials were obtained from the right hand as in our previous studies (Shinohara et al. 2005; Yoshitake and Shinohara 2013). Surface EMG was recorded from the first dorsal interosseus muscle with bipolar Ag–AgCl electrodes (diameter, 8 mm; interelectrode distance, 10 mm) that were attached to the distal portion of the muscle. The electrodes were connected to a differential amplifier (500–1,000×) having a bandwidth of 5–1,000 Hz (Nihon-Kohden MEG-6100, Tokyo, Japan). A bipolar, fine-wire electrode was inserted into the first dorsal interosseus muscle to record MU action potentials. The fine-wire electrode consisted of three insulated stainless steel wires (50 μm diameter; Unique Medical, Japan) that were held together at the recording tip using medical glue. The wires were threaded through the lumen of a disposable 27-gauge hypodermic needle, and a barb of 2 mm in length was created at the tip of the recording end of the electrode. The electrode was inserted into the first dorsal interosseous muscle to a depth
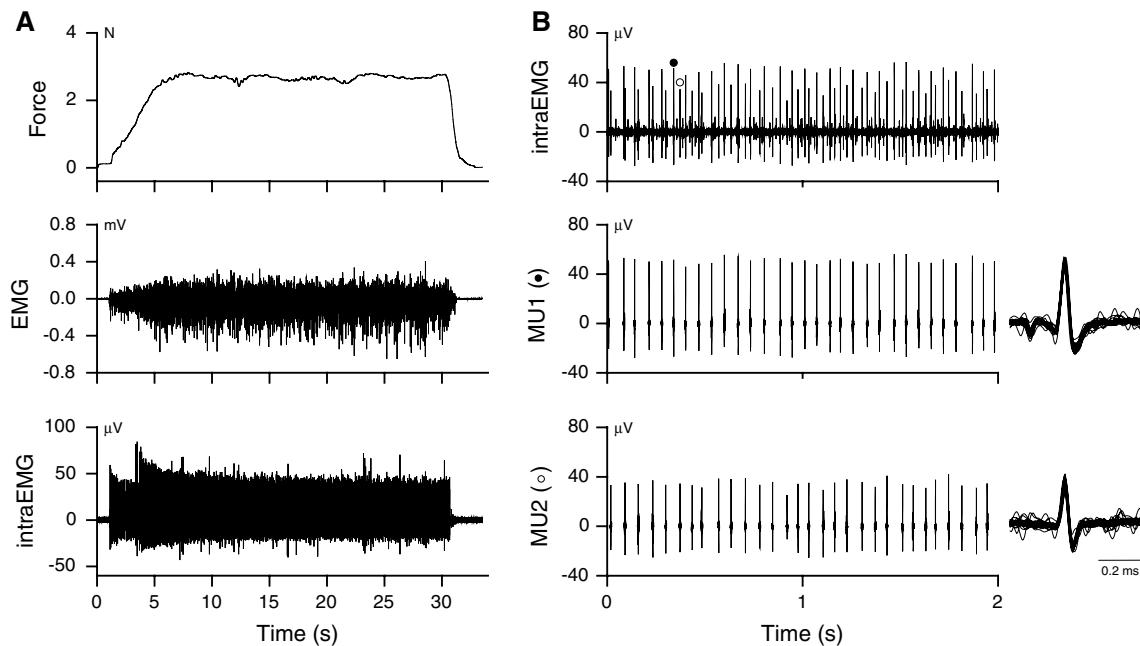
Fig. 1 Representative recorded and analyzed signals during steady contraction. **a** Force (*top row*), surface EMG (*middle row*), and intramuscular EMG (intraEMG, *bottom row*). **b** A portion of intramuscular EMG from **a** (intraEMG, *top row*) and two discriminated action potentials with overlaid waveforms (*middle* and *bottom rows*)

of about 10 mm, and the needle was withdrawn, leaving the wires within the belly of the muscle. Two of the wires were selected for bipolar recording, and the position of these wires was adjusted to record a single MU as clearly as possible for later decomposition of individual MUs. The two wires were connected to a high impedance input module (HZP, Grass Technologies, Warwick, Rhode Island, USA) and then to a differential amplifier (EX1, Dagan Corporation, Minneapolis, Minnesota, USA). The signals were differentially amplified ($2,000\times$) and band-pass filtered (150–10,000 Hz). The signals were collected at a sampling rate of 2,000 samples/s for abduction force, pinch-grip force, and surface EMG and at a sampling rate of 20,000 samples/s for MU action potentials with a 16-bit analog-to-digital converter (Power 1401, Cambridge Electronic Design, Cambridge, England) (Fig. 1a).

Force, surface EMG, and MU action potentials in the middle 16.384 s during single and dual tasks were processed to yield variables of interest (Fig. 1a). As a magnitude measure of neural activity in a pool of MUs, root mean square amplitude (RMS) of surface EMG was calculated. The RMS values of surface EMG during the steady-contraction task were normalized to the corresponding maximal values during the MVC task (% EMGmax). After the force was detrended and low-pass filtered at 5 Hz, the mean and coefficient of variation (CV) of force were calculated (Yoshitake et al. 2008; Yoshitake and Shinohara 2013). The first derivative of force was calculated followed by low-pass

filtering at 5 Hz using a fourth-order Butterworth filter with a zero phase lag (dF/dt) (Yoshitake and Shinohara 2013). Surface EMG was full-wave rectified and smoothed with a Hann-window of 400 ms in duration (rsEMG) (Negro et al. 2009). This smoothing is comparable to a low-pass filtering at approximately 2 Hz (De Luca and Mambrito 1987; Negro and Farina 2012). CV of rsEMG was calculated. Action potentials of MUs were identified based on wave shape, amplitude, and duration using a computerized spike-sorting algorithm (Spike 2. version 7.06a, Cambridge Electronic Design) (Shinohara et al. 2005) (Fig. 1b). For each trial, the inter-spike intervals of discriminated MUs were visually re-examined to ensure discrimination accuracy. When abnormally short (<20 ms) or long (>200 ms) intervals (Negro et al. 2009) were found due to the similar shapes or small amplitude of action potentials, the MU spikes were re-analyzed in a spike-by-spike basis. If the same MU could not be identified throughout the single and dual tasks, the trials were rejected. To analyze low-frequency oscillations in the instantaneous discharge rate of MU, the time-varying instantaneous discharge rate of MU was calculated from the inter-spike interval and smoothed by a Hann-window of 400 ms in duration, as used in previous studies (De Luca et al. (1982); De Luca (1985); Negro et al. 2009) (Fig. 2). The mean and CV of MU discharge rates and MU inter-spike intervals were calculated.

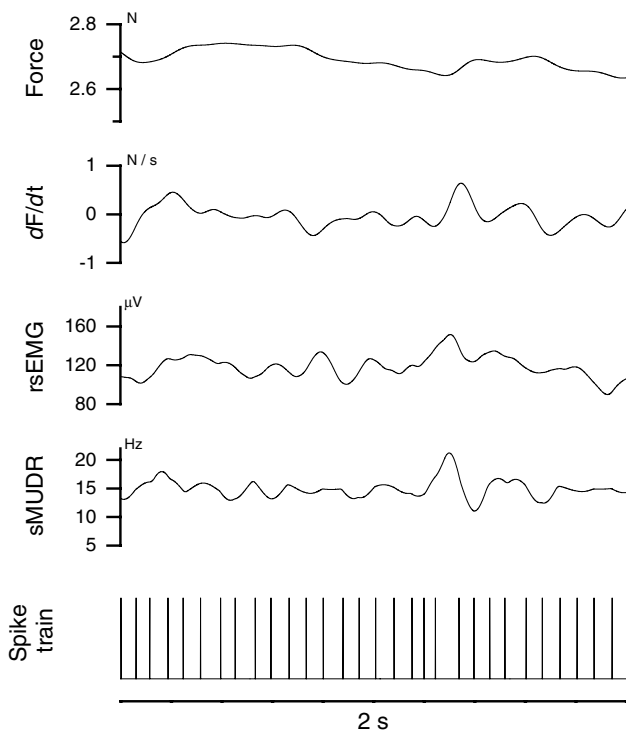To examine the extent of temporal correlations (1) between MU discharge rate and rsEMG, and (2) between

Fig. 2 Force (*top row*), first derivative of force (*d*F/*d*t, *second row*), rectified-and-smoothed EMG (rsEMG, *third row*), smoothed motor unit discharge rate (sMUDR, *fourth row*), and motor unit spike train decomposed from intramuscular EMG (Spike train, *bottom row*)

MU discharge rate or rsEMG and force or *d*F/*d*t, a cross-correlation function (CCF) between the combinations of these signals was calculated according to our previous study (Yoshitake and Shinohara 2013). The simple removal of the DC component was performed before obtaining CCF. From the CCF, a distinct peak above 95 % confidence limit (CCF peak) was identified in the ±100 ms period between neural signals (i.e., MU discharge rate and rsEMG) and in the ±400 ms period between neural and mechanical signals (i.e., force and *d*F/*d*t) (De Luca et al. 1982). The values for CCF peak and time lag were determined subsequently (Semmler et al. 1997). The time resolution of these calculations was 1 ms. The above post-processing of signals was performed using custom-made software (MATLAB, Mathworks, Natick, Massachusetts, USA).

Statistical analysis

Paired Student's *t* test was performed in time lag of the CCF peak, mean and CV of MU discharge rate, RMS of original EMG, CV of rsEMG, and mean and CV of force between the single and dual tasks. The difference in the CCF peak between MU discharge rate and rsEMG between the two tasks were also tested by paired Student's *t* test. To determine significant differences in the CCF peak between

mechanical and neural signals, a three-way analysis of variance (ANOVA) with repeated measures was performed. The three factors for the ANOVA were mechanical signal type (force and *d*F/*d*t), neural signal type (MU discharge rate and rsEMG), and task (single and dual). When appropriate, post hoc comparisons were performed using *t* tests with Bonferroni corrections. An alpha level of 0.05 was chosen for these comparisons. $P < 0.05$ or 0.01 is noted when appropriate. Unless stated otherwise, descriptive data are expressed as mean ± SE in the figures and mean ± SD in the text and table as preferred in our previous studies (Yoshitake et al. 2008; Yoshitake and Shinohara 2013).

Results

Characteristics of fluctuations in motor output

The total number of MUs identified was 14. The target force level for the single and dual tasks ranged from 5 to 20 % MVC, and the target force (8.7 ± 4.7 % MVC when collapsed across tasks) and mean exerted force (8.6 ± 5.5 % MVC) in the right hand were not significantly different between the tasks. As a magnitude measure of neural activity in single MUs, the mean inter-spike interval (single: 74.2 ± 21.9 ms, dual: 73.5 ± 22.5 ms) and the derived mean MU discharge rate (single: 14.5 ± 3.7 pps, dual: 14.8 ± 4.5 pps) were not significantly different between the tasks. As a magnitude measure of neural activity in a pool of MUs, there was no significant difference in RMS of original EMG (i.e., before rectification and smoothing) between the tasks (single: 0.049 ± 0.028 mV or 6.9 ± 4.1 % EMGmax; dual: 0.051 ± 0.028 mV or 7.2 ± 4.2 % EMGmax).

As a measure of oscillations in mechanical output, CV of force was greater by 28 % ($P < 0.01$) in the dual task compared with the single task (Fig. 3). As a measure of oscillations in individual MUs, CV of MU discharge rate was greater by 17 % ($P < 0.05$) in the dual task compared with the single task. CV of rsEMG was greater by 14 % ($P < 0.01$) in the dual task compared with the single task. CV of MU discharge rate was positively correlated with CV of force during single ($r = 0.885$, $P < 0.01$) and dual ($r = 0.832$, $P < 0.01$) tasks, but not significantly correlated with CV of rsEMG.

Temporal correlations between fluctuations in motor output

For the analysis of temporal correlation between the fluctuations in the instantaneous discharge rate of individual MUs and the electrical signal that may reflect neural fluctuations in a pool of MUs, MU discharge rate was positively cross-correlated with rsEMG as confirmed
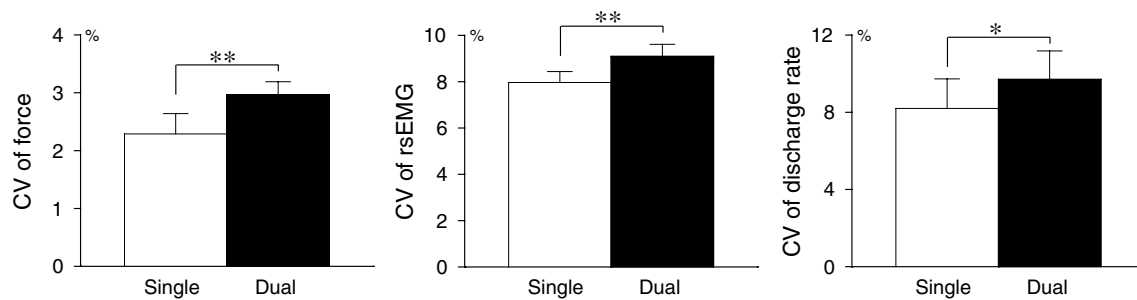
Fig. 3 Variability in motor output during the single (*open bars*) and dual (*filled bars*) tasks. CV of force: coefficient of variation (CV) of force; CV of rsEMG: CV of rectified-and-smoothed EMG; CV of discharge rate: CV of instantaneous MU discharge rate. $*P < 0.05$, $**P < 0.01$
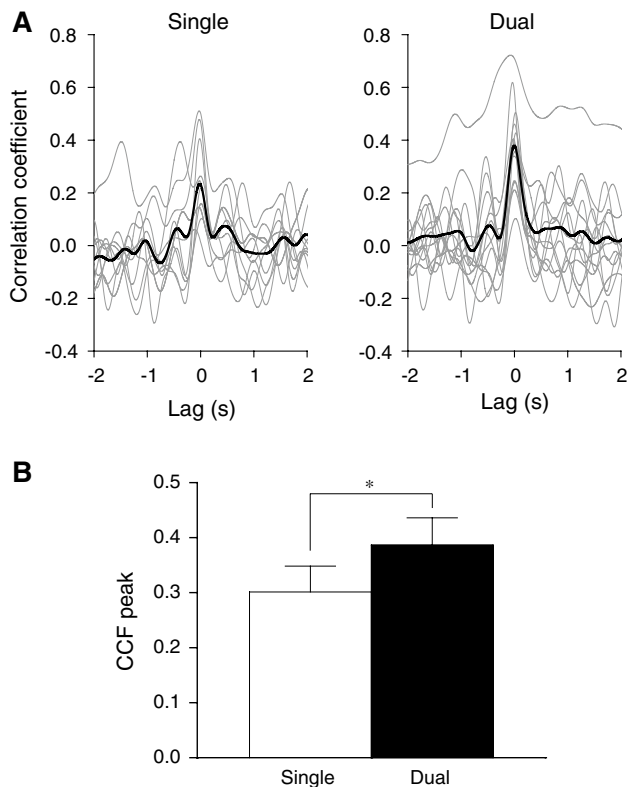

Fig. 4 a Cross-correlation function between the low-frequency oscillations in MU discharge rate and rectified EMG during the single (*left panel*) and dual (*right panel*) tasks across tested motor units. Individual (*thin lines*) and averaged (*thick lines*) time-series traces are shown. **b** Peak value of cross-correlation function (CCF peak) between the low-frequency oscillations in MU discharge rate and rectified EMG during the single and dual tasks. *Open* and *filled bars* represent the data during the single and dual tasks, respectively. $*P < 0.05$

by the significant ($P < 0.05$) and distinct peak in CCF (Fig. 4a) in both tasks. This CCF peak was greater ($P < 0.05$) in the dual task (0.38 ± 0.05) compared with the single task (0.30 ± 0.05) (Fig. 4b). The time lag where CCF peak appeared was -13.0 ± 33.0 ms across

the tasks, with no significant difference between the tasks.

For the analysis of temporal correlations between neural and mechanical signals, MU discharge rate was cross-correlated with force and dF/dt as confirmed by the significant ($P < 0.05$) and distinct peak in CCF (Fig. 5a). There were main effects of mechanical signal type ($P < 0.05$), neural signal type ($P < 0.05$), and task ($P < 0.05$) on CCF peak between mechanical and neural signals (Fig. 5b) while there was no significant interaction. As a main effect of mechanical signal type (force and dF/dt), CCF peak between dF/dt and neural signals (i.e., MU discharge rate and rsEMG) was greater ($P < 0.05$) compared with CCF peak between force and neural signals across tasks. CCF peak between MU discharge rate and the mechanical signals (i.e., force and dF/dt) was greater compared with that between rsEMG and mechanical signals across tasks as a main effect of electrical signal type ($P < 0.05$). As a main effect of task, CCF peak was greater ($P < 0.05$) in the dual task compared with the single task across neural and mechanical signals. Post hoc comparisons revealed that CCF peak between MU discharge rate and dF/dt was greater compared with CCF peak between MU discharge rate and rsEMG ($P < 0.05$) or force ($P < 0.01$) across tasks (Fig. 6).

Discussion

There are three major findings. First, a significant peak was found in the cross-correlation function between the low-frequency oscillations in MU discharge rate and rectified surface EMG. While the low-frequency oscillations in MU discharge rate and rectified surface EMG are distinct measures with respect to their signal recording and processing, the presence of significant correlation between them demonstrates the importance of the neglected low-frequency oscillations in rectified surface EMG for assessing oscillatory input to a motor unit pool. Second, the coefficient of cross-correlation between the low-frequency oscillations
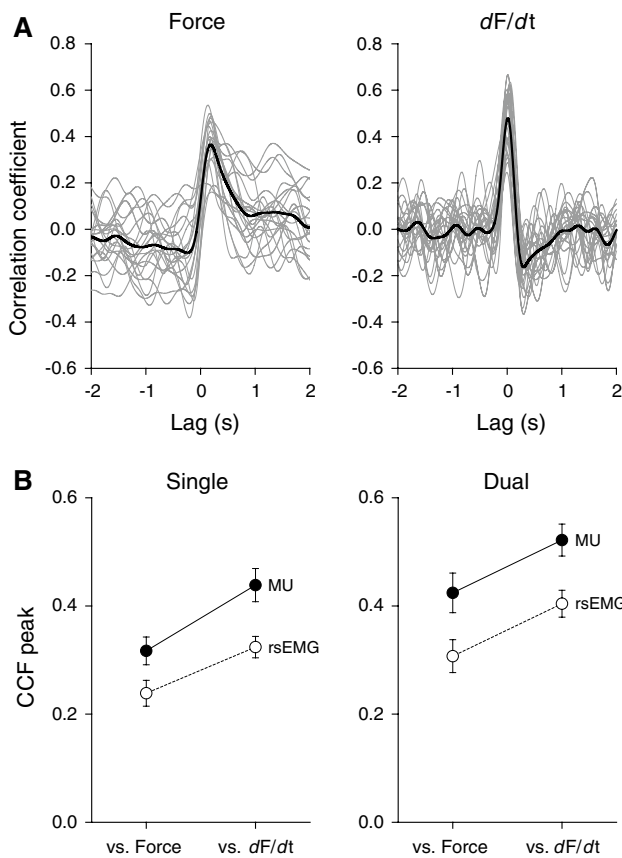
Fig. 5 **a** Cross-correlation function between the low-frequency oscillations in MU discharge rate and force (*left panel*) or *d*F/*d*t (*right panel*) across tested motor units. Individual (*thin lines*) and averaged (*thick lines*) time-series traces are shown. **b** CCF peak between each of the neural signals (MU: low-frequency oscillations in instantaneous MU discharge rate; rsEMG: rectified-and-smoothed EMG) and each of the mechanical signals (Force; *d*F/*d*t: first derivative of force) during the single (*left panel*) and dual (*right panel*) tasks. There were main effects of mechanical signal type ($P < 0.05$), neural signal type ($P < 0.05$), and task ($P < 0.05$)

Fig. 6 CCF peak between instantaneous MU discharge rate and rectified-and-smoothed EMG (rsEMG), force, or *d*F/*d*t. The values are collapsed across single and dual tasks. **P < 0.01

these signals was not readily predictable (see "Introduction"), finding a significant correlation is a novel and meaningful demonstration of the importance of the low-frequency component of rectified surface EMG in assessing low-frequency neural oscillations.

Our hypothesis is supported by the presence of a significant peak in CCF between the low-frequency oscillations in MU discharge rate and rsEMG (Fig. 4). De Luca et al. (De Luca et al. 1982; De Luca 1985; De Luca and Erim 1994) and Negro et al. (Negro et al. 2009) demonstrated that low-frequency oscillations in the instantaneous discharge rate of MU during steady contraction were temporally correlated with low-frequency fluctuations in force. The presence of such a temporal correlation is confirmed in the current study with the significant peak in CCF between the low-frequency oscillations in MU discharge rate and force (Fig. 5). While these previous studies (De Luca et al. 1982; De Luca 1985; De Luca and Erim 1994; Negro et al. 2009) did not examine the utility of surface EMG signal in characterizing the low-frequency oscillations in motor output during steady contraction, we recently demonstrated that rectified and low-pass filtered surface EMG signal is temporally correlated with low-frequency oscillations in force (Yoshitake and Shinohara 2013). Our hypothesis was further supported by the similarity during both single and dual tasks in the relation between the strengths of temporal correlations for low-frequency oscillations in the tested mechanical (force and *d*F/*d*t) and neural (MU discharge rate and rectified surface EMG) signals (Fig. 5b). Hence, the current findings advance the utility of surface EMG signal for assessing low-frequency oscillations in neural activity by providing new evidence that information on low-frequency oscillations in the instantaneous discharge rate of MU is represented in the low-frequency component of rectified surface

in MU discharge rate and *d*F/*d*t was greater compared with that between the low-frequency oscillations in MU discharge rate and force. Third, cross-correlations between MU discharge rate and both force and *d*F/*d*t, as shown in the single task, were preserved and magnified during the dual task when fluctuations in motor output were increased compared with the single task.

Low-frequency oscillations in MU discharge rate and rectified surface EMG

The first purpose of this study was to examine whether the low-frequency component of rectified surface EMG is temporally correlated with low-frequency oscillations in the instantaneous discharge rate of MU during steady contraction. Since the presence of a temporal correlation between
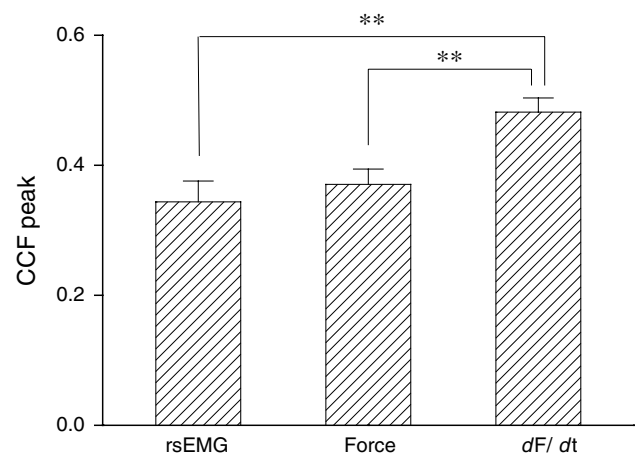
EMG signal, which has been neglected in studying oscillations in motor output (Conway et al. 1995; Baker et al. 1997; Brown 2000; McAuley and Marsden 2000; Johnson et al. 2011).

The degree of temporal correlation between the low-frequency oscillations in the instantaneous discharge rate of individual MUs and rectified surface EMG during steady contraction may be influenced by various factors. Potential factors include the variability of MU discharge rate, the number of MUs, and contraction intensity. These factors can influence the amount of signal components that reflect the low-frequency oscillations in the discharge rate of tested MUs within the rectified surface EMG. The greater CCF peak between MU discharge rate and rsEMG with greater fluctuations in motor output in the dual versus the single task (Fig. 3) implies the influence of the variability of MU discharge rate. Contraction intensity affects the number of recruited MUs and distortion of surface EMG (Keenan et al. 2005, 2006). Additionally, an associated increase in CV of MU discharge rate and CV of rsEMG during the dual task (Fig. 3) indicates associated changes in the magnitude of fluctuations between the low-frequency components of instantaneous MU discharge rate and rectified surface EMG. The current study revealed the temporal correlation of and suggested the associated change in the magnitude of fluctuations between the low-frequency components of instantaneous MU discharge rate and rectified surface EMG. It is probable that the low-frequency component of rectified surface EMG may be used as a noninvasive measure for assessing both the temporal and magnitude characteristics of low-frequency oscillations in neural activity that is represented in the instantaneous discharge rate of MUs.

Temporal correlation between oscillations in MU discharge rate and dF/dt

The second purpose of this study was to examine whether low-frequency oscillations in the instantaneous MU discharge rate are temporally correlated with oscillations in the rate of change in force. Our hypothesis is supported by the presence of a significant peak in CCF between the low-frequency oscillations in MU discharge rate and dF/dt (Fig. 5a). In our previous study that found a significant temporal correlation between rectified surface EMG and dF/dt, we suggested that discharge characteristics of MUs would contribute not only to force but the rate of change in force (Yoshitake and Shinohara 2013). The current findings support this notion by providing direct evidence from the actual discharges of MUs.

While the magnitude of CCF peak between the low-frequency oscillations in MU discharge rate and force in the current study (0.37, see Fig. 6) was comparable to the reported values (~0.41) at similar contraction levels (Negro et al. 2009), the observed CCF peak between the low-frequency oscillations in MU discharge rate and dF/dt showed a greater value (0.48, see Fig. 6). Greater temporal correlation of the low-frequency oscillations in MU discharge rate with dF/dt than with force was already apparent from the visual observation of the time-course signals (Fig. 2). The reason for the greater temporal correlation between the low-frequency oscillations in the instantaneous MU discharge rate and dF/dt during steady voluntary contraction may be inferred from the expected profiles of force and dF/dt during muscle contraction induced by electrical stimulation. When one extra pulse is added to ongoing constant trains of electrical stimulation, force signal is expected to show an abrupt transient increase (Burke et al. 1970). With a subsequent additional pulse before force reaches a peak, the rate of increase in force (dF/dt) will be greater if the interval between pulses is shorter due to summation, and the same would apply for the rate of decrease in force (dF/dt) resulting from successive removal of pulses (Burke et al. 1970). Profiles of muscle force itself are smoother and more prolonged compared with dF/dt. The same principle as in this example for electrically stimulated contraction may underlie the profiles of force and dF/dt during asynchronized activation of MUs in voluntary contraction. This reasoning supports the notion that the oscillations in instantaneous MU discharge rate are associated with dF/dt and are more so than the association with force itself.

The degree of temporal correlations between the low-frequency oscillations in the instantaneous MU discharge rate and dF/dt would be influenced by multiple factors. The factors similar to those of the consideration of its correlation with the low-frequency oscillations in rectified surface EMG include the level of contraction intensity, the number of MUs, and the variability of MU discharge rate. Differing potential factors include the amount and sources of low-frequency force fluctuations. While the current experimental study does not allow for identifying the specific independent factor that determines the degree of correlation, the amount of force fluctuations associated with neural oscillations appears to be involved from the following results. In the dual task, the CVs of force, MU discharge rate, and rectified surface EMG increased compared with the single task. These increases in the variability of motor output resulted in increases in the temporal correlations during the dual task. Moreover, the relations in the magnitude of correlations among the tested signals during the dual task were not different from the single task. Additionally, in other situations where the tested force is the net force produced from multiple muscles (e.g., elbow flexors, knee extensors), the increased number of involved muscles would also attenuate the correlations between the instantaneous discharge rate of MU and dF/dt. Under muscle contractions with

large number of activated motor units or involved multiple muscles, it was generally limited to estimate the precise motor unit discharge in vivo because of difficulties to decompose in dealing with action potential superposition. Assuming that the impact of these modulating factors on the degree of correlation would be clarified and taken into account in future studies, perhaps using simulations, the findings in the current study provide the experimental evidence for supporting the potential utility of dF/dt in assessing the low-frequency oscillations in neural activity that is represented in the instantaneous MU discharge rate.

Among the tested CCF peaks of various combinations, the cross-correlation between dF/dt and MU discharge rate had the highest peak (Fig. 6). The temporal correlation between MU discharge rate and rsEMG was lower, while both are directly related neural signals, when compared with the correlation between MU discharge rate and dF/dt. The lower correlation with MU discharge rate for the rectified surface EMG most likely results from distorted information on the instantaneous MU discharge rate in surface EMG due to signal cancelation of action potentials (Keenan et al. 2005, 2006; Farina et al. 2013). The highest temporal correlation between dF/dt and MU discharge rate lends support to the potential utility of dF/dt as a noninvasive measure for assessing the temporal aspect of low-frequency neural oscillations during steady voluntary contraction. For example, studies that would compare the temporal characteristics of low-frequency neural oscillations in single muscles between the right and left hands could benefit from using dF/dt rather than surface EMG.

In conclusion, the low-frequency oscillations in the instantaneous discharge of motor units are temporally correlated with the low-frequency component of rectified surface EMG as well as with the rate of change in force during steady voluntary contraction of a hand muscle. The findings suggest the potential usefulness of the low-frequency component of rectified surface EMG and the rate of change in force (dF/dt) in assessing the low-frequency oscillations in neural activity that are involved in steady voluntary contraction.

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