Relation between motor unit / muscle activity and fine motor performance

Yasuhide Yoshitake

Department of Sports and Life Sciences, National Institute of Fitness and Sports in Kanoya, 1 Shiromizu, Kanoya, Kagoshima 891-2393, Japan

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Abstract Human movement is a consequence of joint torque or muscle force produced by muscle or muscle groups. Therefore, motor performance in human movements can be determined by the accuracy of joint torque or force produced by muscle/muscle groups. Since motor unit (MU) activity contributes to the force exerted by muscle, the ability to accurately perform steady contractions should be attributed to MU discharge patterns and MU contractile properties. Force fluctuations, which reflect accuracy in fine motor output, can thus affect an individual's motor control abilities, for example, using chopsticks or going for a walk. Accordingly, mechanistic investigations into the characterization of force fluctuations will provide valuable information concerning the modalities needed to improve or regain motor control in healthy and clinical populations. This paper describes the physiological mechanisms responsible for the adaptation of force fluctuations to various environments. Methodologies for analyzing force fluctuations, particularly in multiple muscle systems, are also addressed to provide additional insights into the mechanisms of fine motor control.

Keywords : fine motor control, force fluctuations, electromyogram, motor unit

Introduction

Motor output in humans always involves variability and errors about the intended movement. For example, when an individual tries to match one's output force to a sub-maximal target force as steady as possible with hand, arm or leg muscles, the force exerted by the limb is not constant but rather fluctuates about the target. The amount of fluctuations are influenced by a number of factors including contraction type, the muscle(s) used in accordance to the task, subject age, and activity level of daily life (for review¹⁾). In particular, the force fluctuations for most muscles are greater in older than in younger adults¹⁾, and are furthermore exacerbated by reduced activity (e.g. bed rest), which has been observed in young adults²⁾. Fortunately, these issues can be attenuated with strength training, highlighting the role of physical activity for maintaining or improving motor control ability. Accordingly, it is important to examine the physiological mechanism(s) that are responsible for steady force control, as fluctuations in muscle force during steady contractions impact the ability of individuals to control movements in daily life, such as standing posture³⁾, or hand manipulation tasks⁴⁻⁶⁾.

The activation patterns of motor units (MUs) / muscle(s) should be the final contributor to determine the precision of motor control because muscle force is a consequence of MUs / muscle(s) activity. The current paper, therefore,

highlights findings in literature to examine the relation between MUs / muscle(s) activity and force fluctuations during steady contractions. State-of-the-art techniques used to measure and analyze motor unit activity will also be discussed in part, to provide additional insights into the mechanisms of fine motor control.

Mechanical characteristics of fluctuations in motor performance

In experimental studies examining the mechanical characteristics of fluctuations, a monitor is generally positioned at subject eye level for visual guidance. In this condition, subjects are asked to contract their targeted muscle and to match their force with a target force as steadily as possible for several seconds (Fig. 1). The contraction intensities in the steady-force contraction task have been set within a range of 2.5 to 60% of the subjects maximal voluntary contraction (MVC) force. The ability of individuals to precisely control force during steady muscle contraction has been quantified by the standard deviation (SD) and the coefficient variation (CV) of force in absolute and relative terms, respectively (Fig. 2).

When subjects perform submaximal isometric contractions at a constant force level, the SD of force increases almost linearly with exerted force in all muscle or muscle groups investigated. In contrast, the CV of force is muscle specific. For most muscles and / or muscle groups, the CV of force exhibits a non-monotonic relation with re-

Fig. 1 General experimental setup. Exerted force measured from A) abduction with index finger and B) elbow flexion. Adapted from refs. 11 and 27 with gentle permission.

Fig. 2 A) Raw force (top), surface EMG (middle), and intramuscular EMG (bottom) during steady isometric contractions with first dorsal interosseous muscle. B) Standard deviation (SD) of force (top), coefficient of variation (CV) of force (middle), and amplitude of surface EMG normalized to maximal value. Adapted from ref. 10 and 33 with gentle permission.

spect to force: lower forces tend to exhibit higher CV values (e.g. near 2.5% MVC), but as the force increases, the CV of force tends to decrease^{2,3,7-10} (Fig. 2); whereas in the elbow flexor muscles, the CV of force tends to be less at lower forces and then increases with force¹¹.

When comparing younger and older adults, fine motor performance during steady contractions is not only muscle specific but also task dependent¹. During isometric steady contractions, the CV of force was greater in older adults compared with young adults with the first dorsal interosseus^{7,18}, knee extensor⁹, and planter flexor muscles³⁷, especially at lower forces. However, there was no difference in CV of force exerted by the elbow flexor muscles between young and old adults across a wide range of target forces¹¹. During anisometric contractions, the SD of acceleration for the index finger has been shown to be smaller in constant position tasks (almost isometric contraction) than in slow concentric and eccentric contractions for both age groups¹². In addition, the SD of acceleration of the index finger was greater in older than in younger adults in both constant position and slow anisometric contraction tasks. Moreover, the SD of acceleration for older adults was greater during eccentric contractions compared with concentric contractions. However, there was no such difference for younger adults. Furthermore, as with steady isometric contractions, there was no difference between older and younger adults in the SD of acceleration during slow anisometric contractions with elbow flexor muscles. These results indicate that the amount of fluctuations in force or limb movement (acceleration or displacement) are influenced by age, muscle or muscle groups, and type of contractions.

With respect to anisometric contractions, one might argue that the methods used to detect the mechanical fluctuations in limbs affect the results. For example, Manini et al.¹³ showed a larger SD of displacement during concentric contractions with the knee extensor muscles compared with that during eccentric contractions, whereas Tracy and Enoka⁹ reported no difference between these. Laidlaw et al.¹⁴ showed a larger SD of displacement during eccentric contractions with the first dorsal interosseus muscle compared with that during concentric contractions; but this finding would later be contradicted by Shinohara et al.¹⁵, which reported no difference and showed a greater SD of displacement during concentric contractions¹⁶. When fluctuations in motor performance were evaluated by acceleration measured by an accelerometer attached to a limb, previous studies reported results in contrast to the observed changes in displacement as mentioned above. Previous findings obtained from the first dorsal interosseus muscle indicated that the SD of acceleration is larger during eccentric contractions compared with during concentric contractions^{4,11,15,17}. Theoretically, acceleration is obtained by double differentiation of the displacement, and differentiation would exaggerate higher frequency bands in the source signal. Therefore, the

fluctuations of these different mechanical signals would reflect the different physiological aspects. Additionally, it has been shown that there was considerable difference in the SD of displacement between measurement devices¹⁶. As a consequence, the SD of acceleration could be used as a consistent / reliable measure of fluctuations in motor performance during anisometric contractions compared with the SD of displacement.

Force fluctuations are greater in older adults compared with younger adults¹⁸ (Fig. 3) and are exacerbated by reduced habitual activity (e.g. prolonged bed rest) in young adults² for most muscle / muscle groups. In addition to the unique relation between CV of force and exerted force, however, force fluctuations are not greater for older adults compared with younger adults in a task which requires the performance of low-force isometric contractions for elbow flexor muscles¹¹. The mechanisms of the difference in relation between the amount of force fluctuations and exerted force or in adaptations to age among muscles or muscle groups are not well known, but some

Fig. 3 Mean exerted force (A), standard deviation (SD) of force (B), and coefficient of variation of force (C) during steady isometric contractions. Open circle, data for young adults; Closed circle, data for old adults. Adapted from ref. 18 with gentle permission.

possible causes will be explained at a later part.

On the contrary, the greater force fluctuations due to aging or bed rest (inactivity) can be attenuated with strength training^{2,4,14,19}, indicating the role of habitual activities on force fluctuations. Keen et al.¹⁹ reported that greater CV of force in older adults at low force with the first dorsal interosseus muscle was attenuated by a few weeks of strength training. Moreover, Yan²⁰ indicated that Tai Chi training for 8 weeks reduced the force fluctuations in arm movements. In this study, Tai Chi training did not include any external load. Taken together, it seems that training at high loads may not be necessarily needed to improve force control. In addition, because of the rapid adaptation (2 weeks)^{4,17}, these improvements would be elicited by changes in the nervous system. In line with these assumptions, force fluctuations have been shown to be reduced by practice of a skilled movement without an increase in maximal muscle strength²¹.

Potential mechanisms of force fluctuations

Because muscle force is a consequence of MUs / muscle(s) activity, the mechanisms of force fluctuations should include the contractile characteristics and activation properties of MUs / muscle(s). The force of single MU, estimated by the spike-triggered averaging technique is larger in older adults when compared to younger adults^{7,22}. This adaptation with age could be associated with an increase in the innervation ratio of MUs, which in turn is due to a decline in the number of spinal motor neurons²³. Hence, it can generally be said that larger twitch force from MU contributes to an increase in force fluctuations in older adults. However, it has been shown that 12 weeks of strength-training reduced the amount of force fluctuations in older adults whereas the motor unit force did not change¹⁹. In addition to this, a comprehensive simulation study showed that an increase in motor unit force and decrease in the number of motor units have less influence on force fluctuations during submaximal isometric contractions^{24,25}. In contrast, increases in antagonist muscle activity and motor unit synchronization have been suggested to contribute to an increase in force fluctuations. However, experimental and simulation studies have indicated again that the influence of antagonist activity or motor unit synchronization appears to be negligible during steady isometric contractions²⁴⁻²⁶.

Force fluctuations during steady voluntary contractions are mainly composed of low-frequency oscillations (< 5 Hz, peak power around 2 Hz)^{10,27-29}. 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 Hz²⁷. Experimental studies have also demonstrated that the temporal characteristics of force fluctuations at 1-2 Hz is correlated with the oscillations of the instantaneous MU discharge rate at low frequency, termed common drive³⁰⁻³³ (Fig. 4). Thus,

the low-frequency oscillations in MU activity contribute to force fluctuations during steady contractions^{4,18,27}. These notions were obtained in experiments at least using a single muscle model, such as first dorsal interosseus muscle, which is responsible for most abduction force exerted by the index finger³⁴.

With regards to multiple muscle systems, which are more common in the human body, the mechanisms for force fluctuations during contractions are more complicated^{2,8,9,11,35}. Measurable fluctuations in force reflect the temporal summation of individual forces from multiple muscles, which could not be determined in human experi-

Fig. 4 (A) Discharge frequency records of four concurrently active motor units (dashed lines) and force output (continuous line) recorded during steady isometric contraction. The force level is given as percentage of maximal voluntary contraction (MVC) on the right. (B) Functions obtained by cross-correlating between discharge frequency and (C) between discharge frequency and force. Positive shift of peaks in C indicates that oscillations in discharge frequency leads force fluctuations. Adapted from ref. 30 with gentle permission.

ments. The complexity is already apparent in the behavioral data as mentioned above. For example, the relation between fluctuations in motor output and contraction intensity is variable across different muscle or muscle groups. Moreover, the force fluctuations, expressed as the CV of force, are often greater in older adults compared with young adults, as found in several studies examining abduction of index finger^{1,7,19,36}, knee extension⁹, and plantarflexion³⁷, but not in elbow flexion²⁶ and dorsiflexion³⁷.

Since net force is the summation of individual forces from multiple muscles, the distribution of muscle activity should influence net force fluctuations. In plantarflexion, with the contraction of the triceps surae muscles, force fluctuations have been shown to increase due to reduced habitual activity during 20-day bedrest in healthy young adults^{2,35}. The increase in force fluctuations accompanied a greater increase in the average amplitude of EMG in the medial gastrocnemius (MG) muscle compared with the soleus (SOL) muscle^{2,35}. Based on this finding, it was hypothesized that the activities of MG play a role in augmenting force fluctuations during steady plantarflexion. We tested this by changing the involvement of the bi-articular gastrocnemius muscle with an alteration in the knee joint angle during steady plantarflexion³⁸. As a result, the involvement of the MG was reduced due to decreased fascicle length, increased pennation angle^{39,40}, and decreased motor neuron excitability^{41,42} in a knee-flexed position compared with a knee-extended position. Inconsistent with the hypothesis, fluctuations in net force were lower in the knee-extended position compared with the knee-flexed position. This finding further motivated us to reconsider the potential roles of the MG in modulating fluctuations in plantarflexion force. We speculated that force transmitted from the MG may not fluctuate in the same positive/negative direction or in phase with force transmitted from other plantarflexor muscles, but in a compensatory manner to other plantarflexor muscles. In other words, if the waveforms of force fluctuations in individual muscles are negatively and positively correlated, net force fluctuations obtained in experiments will be reduced and augmented, respectively. In the example for plantarflexion, there may have been a greater amount of negatively correlated fluctuations between the forces from MG and SOL in the knee-extended position compared with the knee-flexed position, resulting in smaller fluctuations in net force. Interestingly, it seems that the CV of force is smaller with an increasing number of agonist muscles⁴³. For example, the average value for the CV of net force for contraction at 5% MVC ranged from 2.6% - 4.3% during abduction of the index finger (a typical single agonist model)^{7,18}, while it ranged 1.1% - 2.1% during knee extension (involving four major agonist muscles)⁹. Therefore, it is possible that the cancellations of force fluctuations from individual muscle heads are more effective with a greater number of involved muscles. In

addition, if a muscle that contains greater force fluctuations ("noisy muscle") is preferentially activated, the net force fluctuations would be greater. Hence, an increase in fluctuations in plantarflexion force with an increase in MG activity after bed rest² may be due to MG acting as a "noisy muscle".

Despite the postulation of these potential mechanisms (temporal association between individual force fluctuations and the preferential activation of "noisy muscle") in multiple muscle systems, these possibilities cannot be examined directly in humans because individual muscle force cannot be measured *in vivo*. To examine these potential mechanism(s), other indirect means, which enable us to estimate the temporal characteristics of individual muscle force, need to be developed.

Assessment of force fluctuations by intramuscular and surface EMG

As stated above, force fluctuations during steady voluntary contractions are mainly composed of low-frequency oscillations (< 5 Hz, peak power around 2 Hz)^{10,27-29}. The low-frequency fluctuations in force are temporally correlated with oscillations of the instantaneous MU discharge rate at low frequency³⁰⁻³³ (Fig. 4). Therefore, it can be hypothesized that force fluctuations can be reconstructed by low-frequency oscillations of the instantaneous MU discharge. Because a multiple number of MUs would be recruited and low-frequency oscillations in individual MU discharge rates are temporally correlated with each other, Negro et al.³² have attempted to extract a purer correlated low-frequency oscillations in the MU discharge rate from multiple recruited MU by using principal component analysis (PCA). As a consequence, the degree of temporal correlation between force fluctuations and PCA-extracted (first principal component) low-frequency oscillations in the MU discharge rate was larger (~63%) compared with that between force fluctuations and low-frequency oscillations in individual MU discharge rates (~41%). More importantly, the degree of this temporal correlation increased with the number of MUs included in PCA. These results suggest that global low-frequency oscillations in the discharge rate of a large number of MUs contribute to force fluctuations. Hence, the degree of fluctuations in individual force could be estimated using this type of signal processing on MU discharges, even in multiple muscle systems.

Detection of MU discharges, however, usually requires invasive procedures using indwelling electrodes. It also has limitations in the range of contraction intensity, the number of samples relative to muscle volume, and the number of muscles detectable, and thus represents only a limited portion of MU pools. In contrast, interference electromyogram, which uses surface electrodes (surface EMG), is noninvasive and less uncomfortable to measure. Additionally, surface EMG includes a summed neural

Fig. 5 (A) Force (top row), rectified and smoothed EMG (second row), smoothed motor unit discharge rate (third row), and motor unit spike train decomposed from intramuscular EMG (bottom row) during steady isometric contraction. (B) Cross correlation function between the low-frequency oscillations in MU discharge rate and rectified EMG during isometric steady contractions across tested motor units ($n = 14$). Adapted and redrawn from ref. 33 with gentle permission.

signal reflecting the number of recruited MUs and their discharge rates. Therefore, surface EMG may be more feasible and useful for understanding the neural oscillations of a pool of MUs during voluntary contractions. In line with a study by Negro et al.³²⁾, Yoshitake et al.²⁸⁾ recently demonstrated that rectified surface EMG in low frequencies (< 5 Hz) was also temporally correlated with force fluctuations during steady voluntary contraction in the first dorsal interosseus muscle. Moreover, Yoshitake et al.³³⁾ demonstrated that low-frequency rectified EMG temporally correlated with low-frequency oscillations in the MU discharge rate (Fig. 5). Hence, surface EMG would be able to reconstruct the force fluctuations of individual muscle because surface EMG reflects low frequency oscillation in the global MU discharge rate of a muscle.

In addition, this temporal correlation was improved by high-pass filtering at around 300 Hz to interference EMG before rectification²⁸⁾. Potvin and Brown⁴⁴⁾ speculated that this pre-processing would improve the signal quality because the low-frequency component of the original surface EMG signals contains the distorted components due to unwanted low-pass filtering when passing from muscle fibers to electrodes, resulting in signal components unrelated to motor unit action potentials. In line with this notion, Riley and colleagues⁴⁵⁾ indicated that high-pass filtering of interference EMG resulted in stronger associations between surface EMG and trains of motor unit action potentials as compared with those obtained from

the standard band-pass filtering (20-800 Hz) of interference EMG. Therefore, high-pass filtering of interference surface EMG before rectification appears to be an effective pre-processing step for extracting small force fluctuations during steady-force contractions, especially at low contraction intensities since EMG has a smaller signal-to-noise ratio at lower contraction intensities²⁸⁾. Hence, it seems that implementation of interference EMG should help to examine the contribution of individual muscle to fluctuations in net force during steady contractions involving multiple muscles.

Conclusion

The physiological mechanisms, being responsible for the steady force control, are very complex and not yet fully understood. For contractions that involve multiple muscles, in particular, the summation of force fluctuations in individual muscles needs to be understood. To this end, the potential utility of signal processing to rectified EMG has been introduced as a new tool for such investigation. However, studies using these new tools are at an early development stage and further studies are needed to establish the applicability of these tools for examining the physiological mechanisms of steady force control.

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