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Transposed firing activation of motor units

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De Luca CJ, Kline JC, Contessa P. Transposed firing activation of motor units. *J Neurophysiol* 112: 962–970, 2014. First published June 4, 2014; doi:10.1152/jn.00619.2013.—Muscles are composed of groups of muscle fibers, called motor units, each innervated by a single motoneuron originating in the spinal cord. During constant or linearly varying voluntary force contractions, motor units are activated in a hierarchical order, with the earlier-recruited motor units having greater firing rates than the later-recruited ones. We found that this normal pattern of firing activation can be altered during oscillatory contractions where the force oscillates at frequencies ≥ 2 Hz. During these high-frequency oscillations, the activation of the lower-threshold motor units effectively decreases and that of the higher-threshold motor units effectively increases. This transposition of firing activation provides means to activate higher-threshold motor units preferentially. Our results demonstrate that the hierarchical regulation of motor unit activation can be manipulated to activate specific motoneuron populations preferentially. This finding can be exploited to develop new forms of physical therapies and exercise programs that enhance muscle performance or that target the preferential atrophy of high-threshold motor units as a result of aging or motor disorders such as stroke and amyotrophic lateral sclerosis.

oscillatory contractions; motor units; firing rate

THE MAJORITY OF STUDIES INVESTIGATING the firing behavior of motor units have been performed in isometric contractions generating constant-force or linearly varying force. In these force paradigms, motor units are recruited in order of increasing size and derecruited in the reverse order, a property known as the size principle (Henneman 1956). The relation between the recruitment and firing rate of motor units is organized in an inverse hierarchical structure, which we refer to as the onion-skin scheme (De Luca and Erim 1994). That is, the firing rates of earlier-recruited motor units have a greater value than those of later-recruited motor units at any time and force during an isometric muscle contraction. [See De Luca and Contessa (2012), De Luca and Hostage (2010), De Luca et al. (1982a,b), Hu et al. (2013b), Masakado et al. (1995), Person and Kudina (1972), and Seyffarth (1940), among others.] Also, all of the motor units in the pool of a muscle receive a common excitation, known as common drive (De Luca et al. 1982b), and modulate their firing rate in unison.

In this study, we wanted to investigate the firing rate and recruitment behavior of motor units when the excitation to the motoneuron pool is continuously altered to produce contractions with oscillating force. Only a few studies have attempted to investigate oscillatory-force production, and those studies

have typically focused on the analysis of the frequency content of the surface electromyographic (sEMG) signal and of the muscle force. In the rare cases where motor unit firings were detected, the number of observed motor units was limited between one and three per contraction (Erimaki and Christakos 1999; Iyer and Christakos 1994; Sosnoff and Newell 2005; Sosnoff et al. 2005; van Bolhuis et al. 1997).

With the development of a sEMG decomposition technology, which has been described in De Luca et al. (2006) and Nawab et al. (2010), it is possible to investigate the firing behavior of a large set of concurrently active motor units during oscillatory contractions. Consequently, we performed this study to investigate whether the recruitment and hierarchical firing rate organization of motor units commonly observed during isometric linearly varying and constant-force contractions is altered during isometric oscillatory-force contractions.

METHODS

The experimental protocols performed in this study were approved by the Institutional Review Board of Boston University. Six subjects, four men and two women, volunteered for the experiment. All read, stated they understood, and signed the informed consent form by the Institutional Review Board of Boston University. Their ages ranged from 21 to 26 yr (23.8 ± 2.0), and all stated that they were free of neuromuscular disorders.

The first dorsal interosseous (FDI) muscle was tested. The hand was secured in a specially designed apparatus that restrained the index finger to isometric contractions. A force gauge measured the force produced by the muscle. It was band-pass filtered from direct current (DC) to 450 Hz and displayed on a computer screen for visual feedback. At the beginning of the experiment, the maximal voluntary contraction (MVC) force was measured. Subjects were asked to contract their FDI muscle maximally for ~ 3 s. Three consecutive trials separated by at least 3 min of rest were collected. The greatest force amplitude of the three trials was designated as the MVC.

The subjects were then asked to track a target force profile displayed on a computer screen. The target profile increased linearly at a rate of 10% MVC/s up to the target level of 20% MVC and remained at this level for 40 s. At the 10-s mark, a 20-s oscillation was superimposed on the force. The amplitude of the oscillation was $\pm 2.5\%$ MVC. The force profile returned to the target level for 10 s and then decreased to 0 at a rate of 10% MVC/s. In subsequent contractions, the oscillation frequency was increased from 0.2 to 0.4, 1, 2, 3, and 4 Hz. The subjects were asked to track the target profile to the best of their ability.

sEMG signals were recorded by an array sensor consisting of protruding blunted pins, each 0.5 mm in diameter, located at the corners and in the middle of a 5×5 -mm square. The signals from four pairs of the sensor electrodes were differentially amplified and filtered with a bandwidth of 20–450 Hz. The four signals were

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sampled at 20 kHz and stored in a computer for offline data analysis. The raw sEMG signals from the four channels of the sensor were decomposed into their constituent motor unit action potential trains (MUAPTs) using the sEMG signal decomposition algorithm described by De Luca et al. (2006) and by Nawab et al. (2010). The validity of this decomposition technique has been independently verified in three different studies by Hu et al. (2013a,b, 2014). The algorithm uses artificial intelligence techniques to identify individual action potentials in the sEMG signal, resolve superpositions, and allocate action potentials to individual motor unit trains. The technique generally extracts the firings of 30–40 MUAPTs from the sEMG signal of a single contraction in the FDI muscle. A verification procedure (De Luca and Contessa 2012; Nawab et al. 2010) was used to calculate the accuracy of the identified firing instances. In this study, only MUAPTs with firing accuracy >90% were considered for further analysis.

The force signal was detrended before computing its frequency spectrum. Epochs of the force were taken during a 10-s interval in the oscillatory-force region. The dominant oscillation frequency during the selected epoch was calculated as the location of the peak of the force spectrum. Note that we discarded from analysis contractions that did not present a peak in the frequency spectrum of the force, i.e., contractions where the oscillation frequency could not be tracked or produced in a consistent manner. We also discarded contractions where the average force deviated from the 20% MVC target value for >2.5% MVC.

The mean firing rate of each motor unit was computed by low-pass filtering the impulse train with a unit-area Hanning window of 2-s duration. For additional details on the filtering procedure, refer to De Luca et al. (1982b). For each motor unit, we calculated the average value of the mean firing rate in a 10-s interval during the oscillatory-force region and in a 5-s interval during the initial constant-force region. We quantified the change in motor unit firing rate that occurred when the force started to oscillate by calculating the difference between these two values, named ΔMFR (in pulses per second or pps). The difference in mean firing rate was plotted as a function of the motor unit recruitment threshold, which was calculated as the force level at which the motor unit began to fire. A linear inverse relation was found when regressing the ΔMFR against the motor unit recruitment threshold. For each subject, the slope and intercept values of the regression lines belonging to different contractions were plotted against the dominant oscillation frequency produced in the oscillatory-force region of the contraction.

We used a recently developed model of motoneuron behavior and force generation (Contessa and De Luca 2013) to investigate whether the control of motor unit firings varies from a feedback-based control during constant or low-frequency force oscillations to a feedforward control paradigm during high-frequency oscillatory tracking tasks, as previously suggested by Sosnoff and Newell (2005) and Sosnoff et al. (2005). To do so, we simulated the firing behavior of all motoneurons in the pool of the FDI muscle in two different conditions: during a constant-force contraction sustained at 20% MVC and during a high-frequency (4.5 Hz) oscillation superimposed on an average target force of 20% MVC, resembling the tracking tasks performed experimentally. In the simulation of constant force, the input excitation to the motoneuron pool of the muscle was adjusted based on the tracking error between the target force and the simulated output force in a force-feedback control condition. In the simulation of the high-frequency oscillation, the force-feedback was disabled, and a fixed “on-off” excitation was imposed as input to the motoneuron pool of the muscle.

RESULTS

Experimental results. The subjects experienced varying degrees of difficulty in performing the oscillatory tasks, but they were generally able to perform oscillations up to 3–4 Hz, with

the exception of one subject who could only produce oscillations up to a frequency of 2 Hz. The black traces in Fig. 1 present examples of the force profiles performed by a representative subject at increasing oscillation frequency; the colored traces present the mean firing rates of a set of decomposed motor units during each contraction.

The force produced by a representative subject is shown in Fig. 2 for increasing frequency of force oscillations. Our data show that subjects were able to track closely the oscillations of the target force profile up to ~ 1 Hz. At these lower frequencies, the spectrum of the force showed a clear peak at the target oscillation frequency (Fig. 2, *middle*), and the sEMG signal amplitude remained consistent and stable throughout the contraction (Fig. 2, *bottom*). At frequencies >1 Hz, subjects experienced increasing difficulty in tracking the target oscillations. The spectrum of the force showed a distinguishable peak near the target frequency along with energy at lower frequencies. The sEMG signal amplitude showed silent periods and signs of on-off activation (Fig. 2), suggesting a different strategy for generating the force oscillations.

We also identified the following surprising alterations in the firing behavior of motor units with increasing oscillation frequency: 1) the firing rates of lower-threshold motor units decreased when the force began to oscillate and returned to their preoscillation level when the oscillation terminated; 2) the decrease was progressively less pronounced for higher-threshold motor units; 3) the decrease was progressively more pronounced at greater oscillation frequencies; and 4) additional higher-threshold motor units were recruited when the decrease in the firing rate of the lower-threshold ones was noted (Fig. 1).

The average force produced by the muscle during the oscillatory region remained, on average, at the target value ($20.2 \pm 0.9\%$ MVC for all contractions). For each motor unit, we measured the decrease in firing rate by calculating the difference between the average firing rate value during the oscillatory-force region and during the initial constant-force region. We found that these differential values were linearly related to motor unit recruitment threshold, i.e., the force at which a motor unit was activated. Also, the slope of the regression lines increased with increasing frequency, whereas the intercept decreased (Fig. 3). The data showed noticeable variability among the subjects, which is expected due to the observed variable quality of the tracking performance during the experiments. Nonetheless, it is apparent that, for all subjects, an oscillation superimposed on a constant-force contraction decreases the firing rate of motor units in a manner that is inversely proportional to their recruitment threshold and that the amount of the decrease is proportional to the dominant frequency of the oscillatory contraction (Fig. 3).

Simulated results. We simulated the firing behavior of all motoneurons in the pool of the FDI muscle when they receive either a force feedback-driven excitation or a predetermined excitation that switches on and off (Fig. 4A2). In the force feedback-driven condition, the value of the excitation required to produce a constant-force level of 20% MVC was 9.4% of the maximal excitation (Fig. 4A2, *left*). In the excitation-driven condition, the excitation was modeled to switch off intermittently to produce force oscillations at 4.5 Hz resembling those of the empirical data (Fig. 4A1). The simulated muscle force (Fig. 4A2) and motor unit firing behavior (Fig. 4B2) obtained in both the constant and the oscillatory-force conditions closely

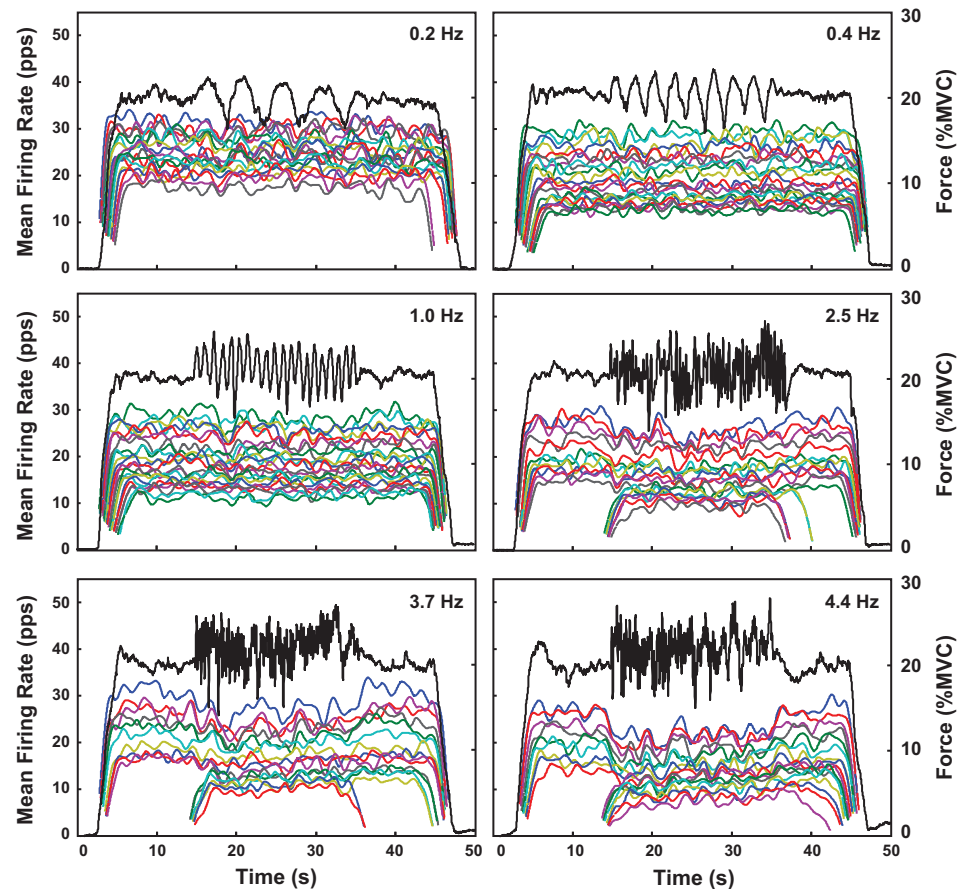


Fig. 1. Force contractions at increasing oscillation frequency. Force trajectory (black line) and motor unit mean firing rates (colored lines), computed by low-pass filtering the firing instances with a 2-s Hanning window, from contractions produced by a representative subject at increasing frequency of force oscillation. The dominant frequency during the oscillatory region is presented in the *top right* corner. One of every 2 identified motor unit is shown for clarity. MVC, maximal voluntary contraction; pps, pulses per second.

resembled those observed in the empirical data (Fig. 4, *A1* and *B1*). The decreasing firing rates of the lower-threshold motor units are evident by the increased interpulse intervals, with intermittent quiescent firing periods corresponding to the decreasing phase of the force oscillations (highlighted in the shaded areas in Fig. 4). Note that to maintain the average force output at 20% MVC during the oscillatory region, the amplitude of the intermittent excitation in the model (Fig. 4A2) is greater (17.4%) than that required to maintain a constant 20% MVC force level (9.4%). This requirement causes the observed recruitment of additional higher-threshold motor units.

DISCUSSION

We have shown that when a subject performs oscillatory contractions at a frequency >1 Hz, a transposition of firing activation occurs, i.e., the firing rates of lower-threshold motor units decrease while new higher-threshold motor units are recruited and increase their firing rate.

This observation was made from motor unit firing instances obtained by decomposing sEMG signals. To eliminate any concerns that the transposition of firing activation might be an artifactual consequence of the decomposition algorithm used to obtain motor unit firing instances from sEMG signals, we collected data from indwelling electrodes during oscillatory contractions. Figure 5 in APPENDIX shows that the same phenomenon was observed among motor units decomposed from intramuscular EMG (iEMG) signals recorded during high-frequency oscillatory contractions. This confirmation provides

evidence that the observed transposition of motor unit firing rates is a real physiological phenomenon.

The transposition of firing rate activation, with lower-threshold motor units decreasing their firing rate concurrently with higher-threshold motor units being recruited and increasing their firing rate, gives the impression that the common drive and onion-skin properties of motor unit firing are disrupted. The common drive property (De Luca et al. 1982b; De Luca and Erim 1994) states that during isometric contractions motor units modulate their firing rates in unison in response to changes in the excitation to the motoneuron pool. The onion-skin property (De Luca et al. 1982a; De Luca and Erim 1994) states that the firing rates of motor units are organized such that the earlier-recruited motor units are always greater than those of the later-recruited ones.

In actuality, the onion-skin and the common drive properties are not disrupted. Consider the following reasoning. We begin by noting that in our study the strategy for force generation appears to shift from a feedback-based visual tracking in low-frequency (<2 Hz) contractions to a feedforward control in oscillations at frequency ≥ 2 Hz that cannot be easily tracked. These observations are in agreement with the findings of others who have studied similar contraction paradigms. For examples, see Sosnoff and Newell (2005) and Sosnoff et al. (2005). At oscillation frequencies that can be visually tracked, the firing rates smoothly lead the force oscillations, and the normal hierarchical characteristics of the firing rate are maintained in the same manner as if the contraction force were maintained constant. When the oscillation frequency is greater

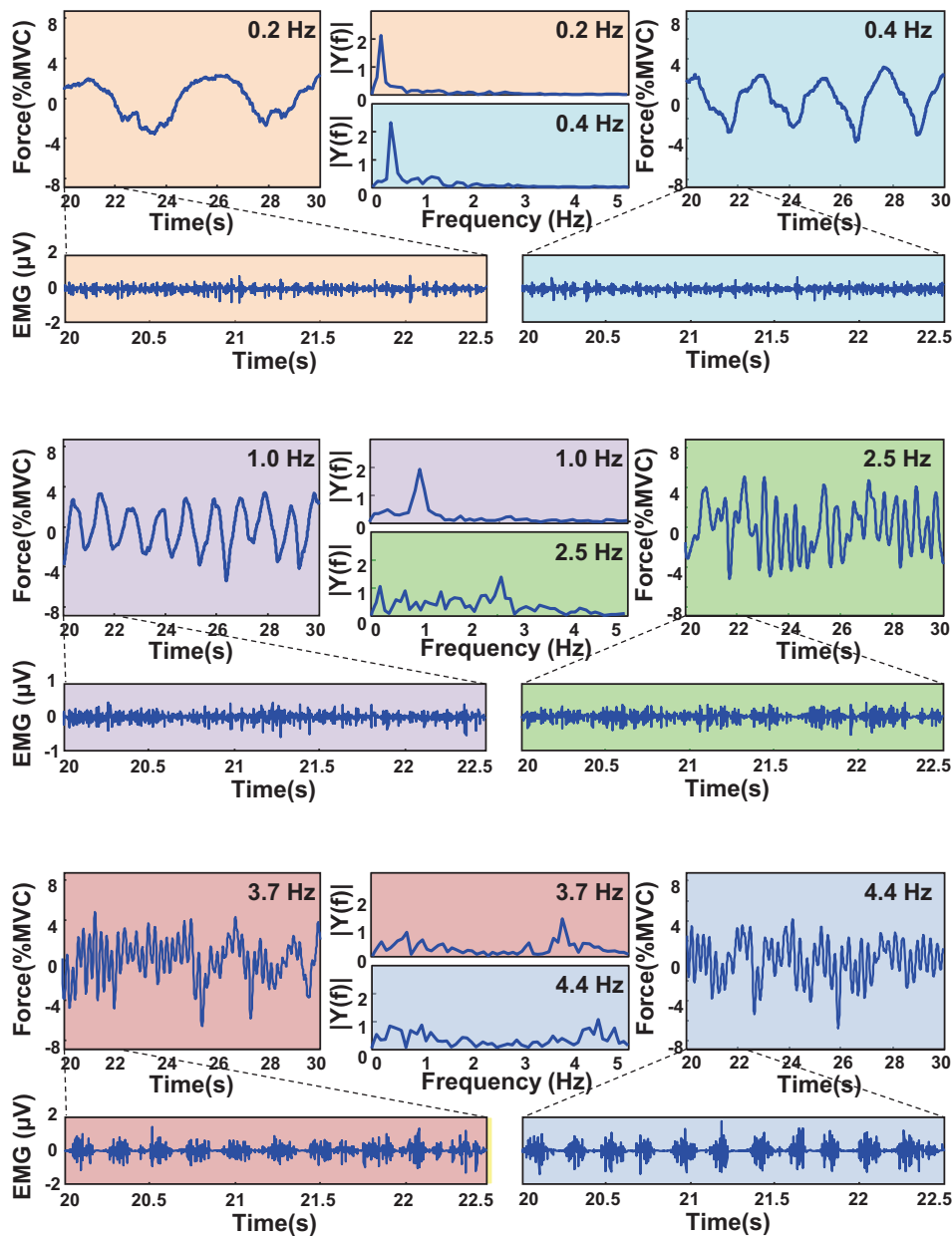


Fig. 2. Force and surface electromyographic (sEMG) signal at increasing oscillation frequency. A 10-s expansion of the oscillatory force produced by a representative subject is shown here with the peak location of the Fourier transform of the force indicated in the *top right* corner. The *middle* shows the force spectrum ($|Y(f)|$) in the oscillatory region with the location of the peak indicated numerically. The *bottom* contains a 2.5-s expansion of the sEMG signal during the oscillatory region. Colors indicate signals generated from the same contraction.

than that which can be visually tracked (~ 2 Hz), the activation strategy appears to change to an on-off pattern. As a result, the active motor units show an on-off firing behavior as evidenced by the sequential periods of activity and quiescence in the sEMG signal (Fig. 2). The influence of the on-off excitation on the firing rates appears to be greater for the lower-threshold motor units because, at the 20% MVC target force level, they fire at greater rates (20–30 pps) than the higher-threshold motor units (5–10 pps). Consequently, more firings per unit time are absent for the lower-threshold motor units, hence their average firing rate decreases more. The average interpulse interval of the higher-threshold motor units is approximately 100–200 ms, which is the same duration of the descending phase of the oscillation at 2–4 Hz (125–250 ms), during which these motor units would be deactivated. Consequently, their average firing rate would not be noticeably affected, and the firing pattern would appear as not being interrupted.

This hypothesis was tested and proved with the use of the force generation model (see the results presented in Fig. 4). At high oscillation frequencies, the feedback-based tracking mechanism that drives force production during constant or slow-varying contractions is disabled. Instead, a feedforward mechanism that includes an on-off excitation is capable of providing motor unit firing rate and force behavior consistent to those observed in the empirical data. All experimental observations were replicated: motor units decrease their firing rate, the decrease is more pronounced for earlier-recruited motor units, while additional later-recruited motor units are activated and increase their firing rates.

Importantly, the force-generation model incorporates the notions describing the common drive and onion-skin properties. Despite the inclusion of the hierarchical organization of motor unit firing behavior, the force-generation model predicts the transposition of motor unit firing activation. These results

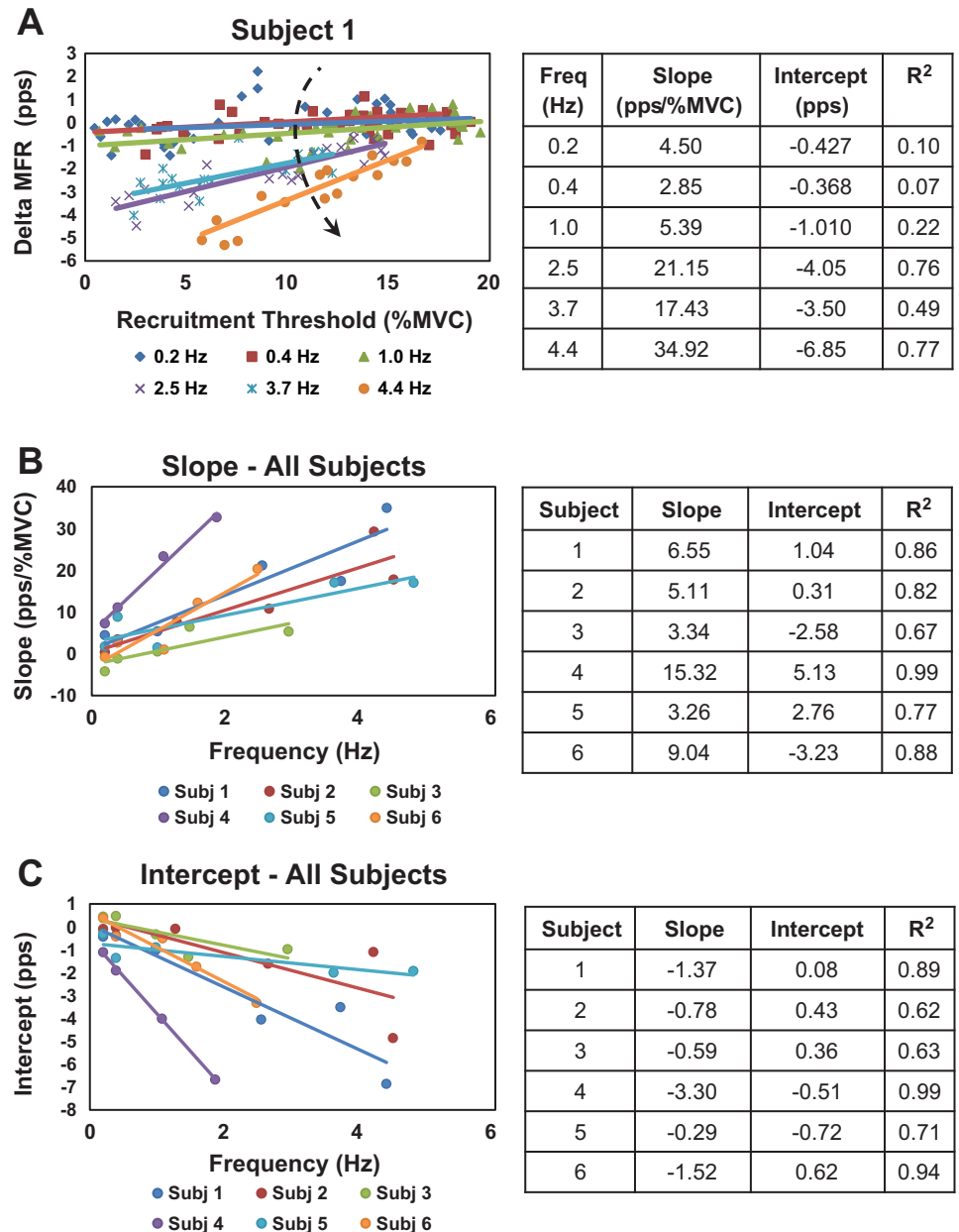


Fig. 3. Mean firing rate decrease at increasing oscillation frequency (Freq). *A*: motor unit mean firing rate decrease during the oscillatory-force region (Delta MFR) as a function of motor unit recruitment threshold for a representative subject. Different colors indicate contractions at different oscillation frequency. *B* and *C*: slope and intercept of the regression lines shown in *A* as a function of oscillation frequency for all 6 subjects (Subj; represented with different colors). The slope, intercept, and r^2 values of the regression lines for the individual subjects are shown in the companion tables on the right.

provide additional proof that this transposition does not derive from a contradiction of the common drive or of the onion-skin properties of the firing rates of motor units. An on-off pattern of input excitation to the motoneuron pool of the muscle is sufficient to explain the observed transposed firing activation of motor units without requiring any special or selective inhibition or excitation to individual motor units.

Note that the force model was developed based on empirical data obtained from linearly varying and constant-force contractions. Nonetheless, we can use this model to test our hypothesis that an on-off excitation reproduces the transposition of firing activation during fast oscillatory contractions with no modification required to the firing properties of motor units. This is because our goal is to estimate the firing behavior of motor units when they are driven by a predetermined on-off excitation with no influence of force feedback or rate of force change.

Also note that the input excitation increases during the positive phases (on intervals) of the fast oscillation to maintain the average force at a constant level. This increase causes the recruitment of additional higher-threshold motor units. Several factors likely contribute to the increased excitation during fast oscillations, possibly including the need to compensate for the absence of excitation during the off intervals and an increased contribution to the net torque from the antagonist muscle.

The above explanation for the transposition of firing activation, relying on the relationship between the firing characteristics of motor units and the on-off disruption of their activation, appears to be cogent. Nonetheless, let us review the likelihood that other potential causes might explain our observations. One potential cause is recurrent inhibition. However, several reports by Baldissera et al. (1981), Horner et al. (1991), Katz and Peirrot-Deseilligny (1998), and Katz et al. (1993) have provided evidence that recurrent inhibition does not act

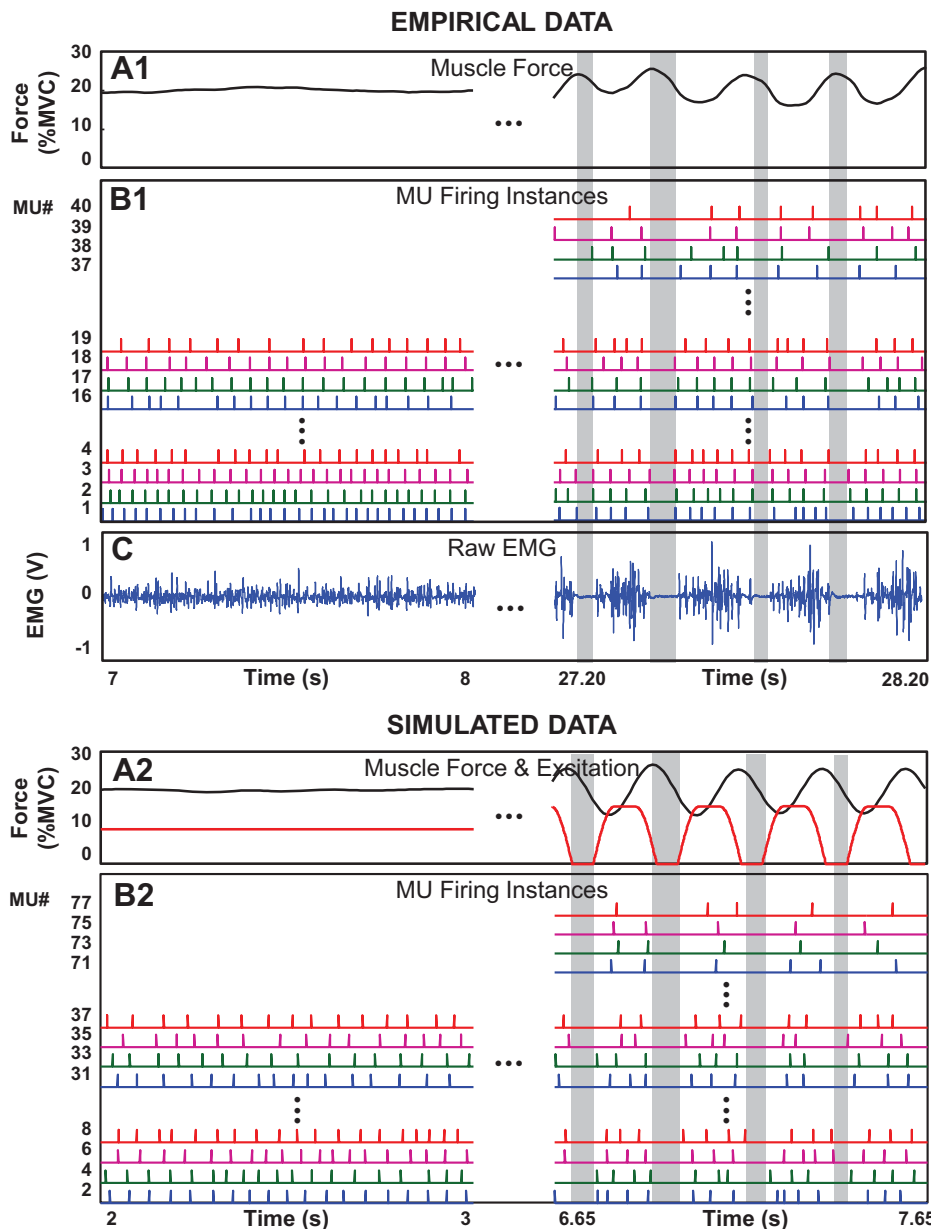


Fig. 4. Force generation strategy during high-frequency oscillations. Empirical Data contains data from a representative subject, whereas Simulated Data contains data obtained by simulating a similar contraction with a model during 1 s of constant-force contraction (left) and 1 s of oscillatory contraction at 4.4 Hz (right). *A1* and *A2*: force produced by the 1st dorsal interosseous (FDI) muscle (black) and simulated excitation to the motoneuron pool (red). *B1* and *B2*: firing instances of a subset of motor unit (MU) firing trains from 5 lower-threshold, 5 intermediate-threshold, and 5 higher-threshold motor units. *C*: raw sEMG signal collected during the force epoch of *A1*.

on motoneurons of the FDI or other intrinsic muscles of the digits. Thus it is unlikely that recurrent inhibition is responsible for the transposition of the firing rates of the motor units of the FDI muscle at fast oscillations.

Alternatively, it might be possible that inhibitory influence from muscle spindles of the FDI during rapid isometric contractions combined with reciprocal inhibition from muscle spindles of the antagonist muscle, the second palmar interosseous, contributed to transposition of the motor unit firing rates and to the observed quiescent periods in the sEMG. However, it is unlikely that the relatively few spindles from the FDI and second palmar interosseous muscles could alone be responsible for silencing FDI motoneurons during the high-frequency oscillatory contractions shown in Figs. 1 and 4. An anatomic study by Smith and Marcarian (1966) found that the FDI contains only ~34 spindles, and the second palmar interosseous contains only ~9. These values are more than an order of magnitude lower than those in other muscles such as the vastus

lateralis (VL) with 440 spindles (Voss 1956). De Luca and Kline (2012) demonstrated that muscles with fewer spindles, such as the FDI, manifest relatively negligible decreases in motoneuron output as a result of spindle inhibition. In contrast, muscles with more spindles, such as the VL, manifest as great as 40% reduction in motoneuron output from spindles.

Another potential factor influencing the transposition phenomenon could be the involvement of Golgi tendon organs, but little information is known about their behavior during voluntary isometric contractions. Any potential contribution from these proprioceptors would be included in the net excitation responsible for the on-off activation that we observed and thus would not negate our explanations of the transposition phenomenon of the motor unit firing rates.

In conclusion, our results indicate that motor units of the FDI muscle manifest an altered on-off activation strategy during oscillatory isometric contractions at frequencies ≥ 2 Hz, which effectuates quiescent periods in the sEMG signal and

a transposition in the firing rates of motor units. This transposition is manifested in a decrease in the firing rates of lower-threshold motor units and the temporary activation of higher-threshold motor units.

Our data show that the hierarchical regulation of motor unit firing activation can be manipulated during high-frequency oscillatory contractions to provide an opportunistic access to increasing the activation of higher-threshold motor units while decreasing the activation requirements of lower-threshold ones. The observed phenomenon has the potential of providing a new modality for reducing overuse of the low-threshold fibers in neurologically impaired individuals such as in post-polio (Grimby et al. 1996) and amyotrophic lateral sclerosis (Vucic et al. 2007) patients, who are affected by progressive degeneration of motoneurons leading to atrophy, weakness, and fatigability. It could also benefit workers engaged in low-force repetitive tasks who are more prone to develop stress-induced pain (Hägg 1991). Targeted training of the higher-threshold motor units could provide countermeasures for the muscle atrophy and preferential deterioration of type II muscle fibers that accrues with advancing age (Stålberg and Fawcett 1982), stroke (Dattola et al. 1993), and amyotrophic lateral sclerosis (Vucic et al. 2007). Preferential training of the high-threshold bigger-size and greater-force-generating motor units could also prove valuable for healthy individuals and athletes wishing to augment muscle force and improve performance of explosive contractions such as those required in weight lifting, jumping, or sprinting.

APPENDIX

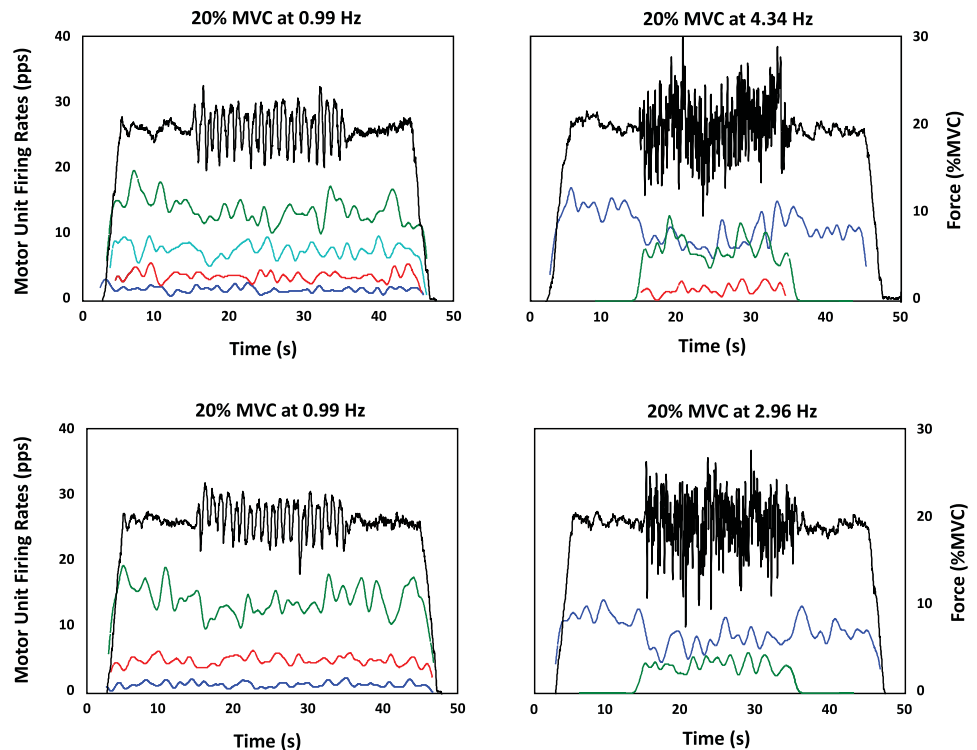
Transposition phenomenon observed in both sEMG and iEMG signals. A subject of the study (male, 26 yr old) performed oscillatory contractions while the sEMG and the iEMG signals were simultaneously recorded. The sEMG signal was recorded using the

five-pin array sensor and analyzed as previously described in METHODS. The iEMG signal was recorded using a quadrifilar, fine-wire sensor inserted directly beneath the surface array sensor. Each electrode consisted of four 50- μm -diameter, nylon-coated NiCr wires (Stabloom 800A; California Fine Wire) glued together. The fine-wire electrode was inserted into the muscle via a 25-gauge disposable hypodermic needle, which was withdrawn leaving the electrode in place. Four combinations of wire pairs were selected and differentially amplified to yield four separate iEMG channels. The signals were band-pass filtered (20–1,750 Hz) to accentuate the differences in the motor unit action potential shapes, sampled at 20 kHz, and independently decomposed. The subject performed the oscillatory contractions presented in METHODS at 20% MVC target force level. One contraction was at a low (~ 1 Hz) and one at a high (~ 3 Hz) oscillation frequency. In addition, the subject repeated the contractions at a lower target force level of 10% MVC to increase the chance of identifying individual motor units in the iEMG signal.

The mean firing rates of the motor units decomposed from the iEMG signal were computed by low-pass filtering the impulse trains with a unit-area Hanning window of 2-s duration (De Luca et al. 1982b) and are presented in Fig. 5. It can be seen that the firing rates of the motor units obtained from the iEMG signals show the same activation pattern as those of the motor units obtained from the sEMG signals (see Fig. 1). The activation pattern is not altered during the lower-frequency (0.99 Hz) oscillation: motor units maintained their average firing rate throughout the contraction, and no new motor units were noted to be recruited during the oscillation. In contrast, the phenomenon of the transposition of firing activation is clearly noticeable at the higher-oscillation frequency (≥ 3 Hz), when low-threshold motor units decreased their firing rates while high-threshold motor units were temporarily activated during the oscillatory part of the contraction. These results prove that the transposition of motor unit firing rates occurs during oscillatory contractions and is not a phenomenon imposed by the process of decomposition sEMG signals.

We also compared the similarity of the motor unit firings detected from the decomposition of sEMG and iEMG signals recorded during the same contraction based on a two-source test (De Luca et al. 2006).

Fig. 5. Transposition phenomenon observed from intramuscular EMG (iEMG). Force trajectory (black line) and motor unit mean firing rates (colored lines), computed by low-pass filtering the firing instances with a 2-s Hanning window, from contractions produced by 1 subject at low (~ 1 Hz, *left*) and high (≥ 3 Hz, *right*) frequency of force oscillation. The motor unit firing instances were obtained by decomposition of iEMG signals recorded from the FDI muscle through fine-wire electrodes. The motor unit firing pattern observed in these iEMG data is similar to that shown in Fig. 1 for sEMG data with the transposition phenomenon becoming evident at high oscillation frequency in both sets of data.



It was expected that some of the active motor units would contribute to the EMG signals of both sensors, whereas some would contribute to the signal of only the sEMG or iEMG sensor, respectively, based on the position of their fibers relative to the sensors.

The drawback of the two-source test comparison is that only very few motor units are typically found in common between the sEMG and the iEMG signals; one per contraction in this study. An additional drawback of this test is that the fast oscillation frequency renders the iEMG signal unstable, with muscle fiber movement causing displacement of the fine-wire electrode inserted in the muscle. Given the added difficulty notwithstanding, we were able to identify one motor unit in two different contractions that was common to both the sEMG and the iEMG signals. One was identified during a 4-s interval in a contraction performed at 0.99 Hz and one during a 6-s interval in a contraction performed at 4.93 Hz. The firing times of the common motor units in the two contractions are shown in Fig. 6, *D* and *E*. The raw sEMG and iEMG signals (Fig. 6, *B* and *C*) and the force produced (Fig. 6*A*) in the identified intervals are also shown.

The similarity among the firings in the two records was high. The accuracy between the two signals, computed as described in De Luca and Contessa (2012), is 94.9% for the low-frequency contraction and 95.5% for the high-frequency contraction. Given these examples, it is apparent that the sEMG decomposition algorithm can accurately decompose contractions oscillating at high-frequency and that the transposition phenomenon is not a product of the decomposition algorithm.

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GRANTS

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DISCLOSURES

C. J. De Luca is the President of the company that developed the technology for decomposing the sEMG signals and the President of the Neuromuscular Research Foundation.

AUTHOR CONTRIBUTIONS

C.J.D. and J.C.K. conception and design of research; J.C.K. and P.C. performed experiments; J.C.K. and P.C. analyzed data; C.J.D., J.C.K., and P.C. interpreted results of experiments; P.C. prepared figures; C.J.D. and P.C. drafted manuscript; C.J.D., J.C.K., and P.C. edited and revised manuscript; C.J.D., J.C.K., and P.C. approved final version of manuscript.

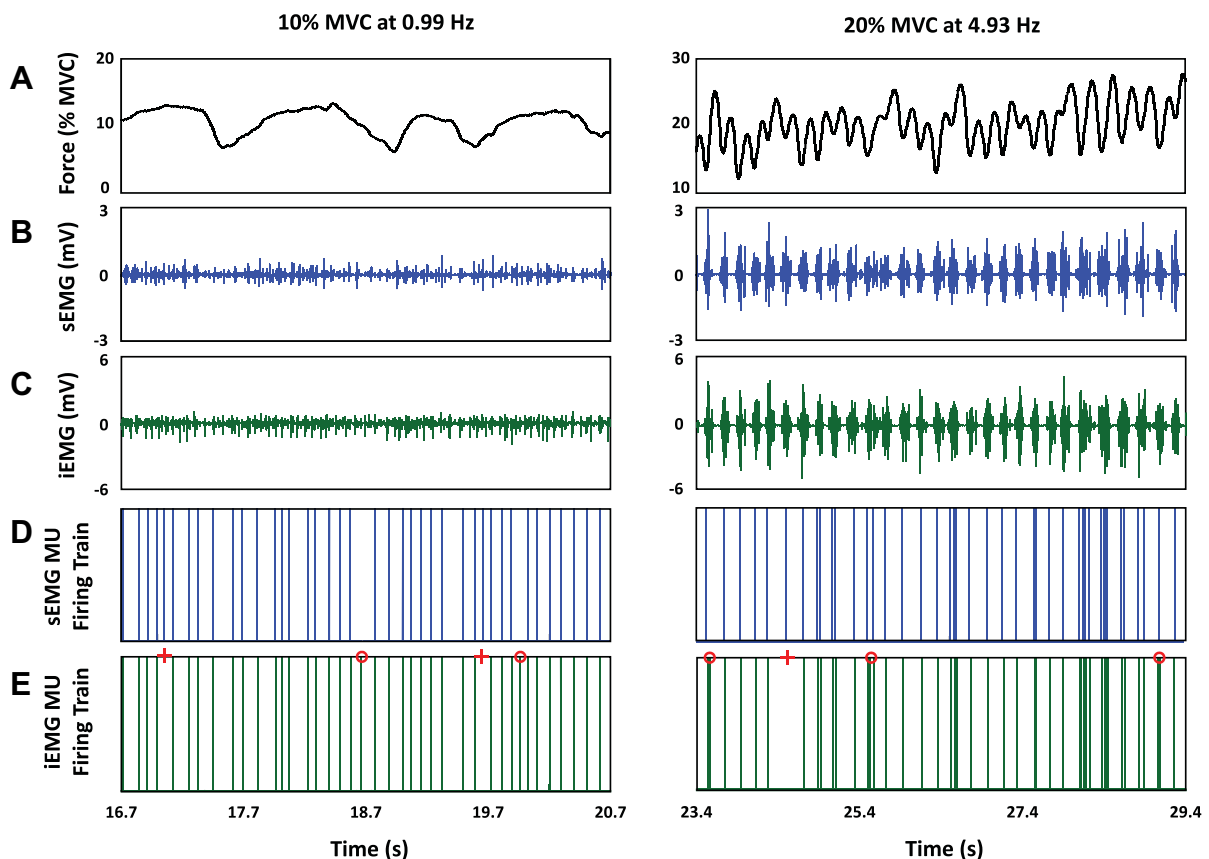


Fig. 6. Similarity among the firings obtained through simultaneous recording of sEMG and iEMG signals. A low-frequency contraction at 10% MVC (*left*) and a high-frequency contraction at 20% MVC (*right*) were performed by a subject while sEMG and iEMG signals were simultaneously recorded from the FDI muscle: the force trajectory (*A*), raw sEMG signal (*B*), raw iEMG signal (*C*), firing train of a motor unit decomposed from the sEMG signal (*D*), and firing train of a motor unit decomposed from the iEMG signal (*E*). Two motor unit firing trains common to both the sEMG and iEMG signals were found in a 4-s interval for the 10% MVC contraction and in a 6-s interval for the 20% MVC contraction. A high degree of similarity between the firings of the 2 motor unit action potential trains can be observed; they have a coincidence of 94.9 and 95.5%, respectively. Red crosses on the *bottom* indicate missed firings, i.e., firings in the decomposition of the sEMG that were not found in the decomposition of the iEMG. Red circles indicate extra firings, i.e., firings in the decomposition of the iEMG that were not found in the decomposition of the sEMG.

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