Effects of Prolonged Vibration on Motor Unit Activity and Motor Performance

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ABSTRACT

SHINOHARA, M. Effects of Prolonged Vibration on Motor Unit Activity and Motor Performance. *Med. Sci. Sports Exerc.*, Vol. 37, No. 12, 2120–2125, 2005. Excitatory input to the α motor neuron pool from Ia afferents is enhanced by brief vibration, yet is depressed when vibration is applied for prolonged periods. The purpose of this article is to synthesize recent findings from several studies on the effects of prolonged vibration on motor unit activity and motor performance during maximal and submaximal contractions in humans. Prolonged vibration does not alter voluntary drive during maximal contractions, but it does reduce Ia afferent input to α motor neuron pools and discharge rate of motor units in the vibrated muscles, leading to a reduction in maximal voluntary contraction force. Alterations in the activity of the motor unit pool may be variable across synergistic muscles due to potential neural connections between synergistic muscles. Prolonged vibration reduces the force fluctuations during submaximal steady contractions, presumably due to a depression of group Ia feedback from leg muscles. When prolonged vibration evokes a tonic vibration reflex in a hand muscle, the mean discharge rate of motor units during a submaximal force-matching contraction increases, leading to an increase in the associated force fluctuations. In summary, prolonged vibration modulates Ia feedback and motor unit activity, which leads to reduced peak force during maximal contractions and altered force fluctuations during submaximal contractions. **Key Words:** REFLEX, STRENGTH, STEADINESS

Human movements are controlled by the integration of the motor command and sensory input, and muscle vibration is known to modulate sensory input from the muscle. Motor performance, such as peak force during a maximal voluntary contraction (MVC) and fluctuations in force during submaximal contractions, is influenced by the pattern of motor unit activity in the responsible muscles (20,28). Motor unit activity is determined by the integration of excitatory and inhibitory neural inputs to the α motor neuron. The major neural inputs to the α motor neuron include: motor command from the supraspinal cortex (excitatory), Ib afferents from the Golgi tendon organ via interneurons (inhibitory), and the Ia afferents from the intrafusal muscle spindle (excitatory) that receive presynaptic inhibition (Fig. 1). Among these neural inputs, the Ia afferents provide information on small length changes in the muscle fiber that are sensed by the intrafusal muscle spindle.

Because the muscle spindle is sensitive to small changes in muscle length, the discharge rate of the muscle spindle is strongly modulated by muscle vibration, which induces repeated changes in muscle fiber length. In a study on the cat soleus muscle (4), the discharge rate of Ia afferents increased linearly with the frequency of vibration up to 500 Hz. When the amplitude of the vibration was large enough, the muscle spindle discharged in response to every stretch of the muscle fiber by the vibration. In humans, effects of brief vibration were observed as enhanced Ia discharges in the tibialis anterior and extensor digitorum longus muscles (23). The Ia afferents driven by the tendon vibration discharged in a one-to-one manner up to 180 Hz in some cases, and most of the Ia afferents discharged harmonically with the vibration up to 80 Hz (23). Depending on the amplitude of vibration, the excitatory input from the vibration-induced Ia afferents can activate the homonymous motor units, resulting in an increase in EMG and force (tonic vibration reflex) (8). In addition, vibration increases the discharge rate of motor units during voluntary contractions of the fatigued muscle (1,11). Hence, brief vibration increases excitatory input to α motor neurons from Ia afferents. Last, brief vibration can induce self-sustained discharge of the motor unit after vibration (16); however, this review focuses on other mechanisms due to the limited investigation of vibration-induced plateau potentials in humans.

An increase in excitatory input to α motor neurons by brief vibration turns into a decrease in excitatory input when the vibration is sustained for more than 10–20 s. After 30-s vibration at 80 Hz, resting discharge rate of the muscle spindle decreased in most of the Ia fibers (73%) originating from multiple leg muscles (22). In addition, a reduction in the short-latency stretch reflex was observed in the soleus muscles after 15-min tendon vibration at 90 Hz (3). These reductions in the feedback transmitted by group Ia afferents are due to 1) increased discharge threshold of Ia fibers (13), 2) presynaptic inhibition of Ia terminals (14), and 3) transmitter depletion at Ia synapses (7) (Fig. 1) after prolonged vibration. Due to the strong effect of vibration on the dis-

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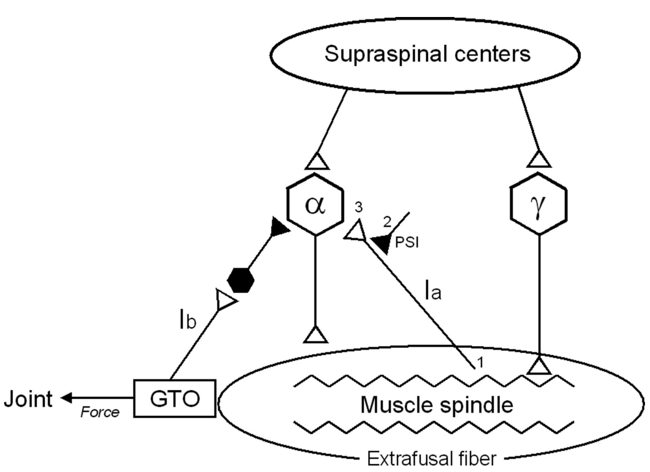

FIGURE 1—Schematic diagram of the neural connections that can be influenced by vibration. Three potential sites that may be influenced by prolonged vibration are located by numbers 1–3. α, α motor neuron; γ, γ motor neuron; Ia, group Ia afferent; Ib, group Ib afferent; PSI, presynaptic inhibition; GTO, Golgi tendon organ.

charges of Ia afferents, it is likely that motor unit activity and motor performance are modulated by vibration. The purpose of this article is to synthesize recent findings from several related studies on the effects of prolonged vibration on motor unit activity and motor performance during maximal and submaximal voluntary contractions in humans.

MAXIMAL CONTRACTION

Impairment in maximally activated motor units.

The effect of prolonged vibration on motor unit activity during maximal contractions has been demonstrated in the tibialis anterior muscle (2). Excitatory input to the α motor neuron pool from Ia afferents is reinforced by concurrent activation of α and γ motor neurons during voluntary contractions. Hence, a reduction in Ia afferent activity depresses motor unit activity during a maximal contraction. For example, Bongiovanni et al. (2) applied 150-Hz vibration over the tendon of ankle flexor muscles for approximately 100 s during repeated MVC and examined the discharge rate of single motor units in the tibialis anterior muscle and peak ankle flexion force. Both low-threshold (<5% MVC) and high-threshold (>50% MVC) motor units reached discharge rates of approximately 35 Hz during brief MVC without vibration (Fig. 2). With tendon vibration, however, the discharge rate of high-threshold motor units declined as vibration was prolonged. The mean discharge rate of high-threshold motor units decreased to approximately 5 Hz, and the peak force decreased by 25%. The discharge rate of low-threshold motor units declined to 30 Hz, which was much less than that of high-threshold motor units. The discharge rate of these motor units was restored after vibration was removed. These results indicate that there is a reduction in the excitatory input from Ia afferents to the α motor neuron pool during maximal contractions. In addition, the vibration-induced reduction in the discharge rate of motor units appears to be more prominent in high-threshold motor units compared with low-threshold motor units.

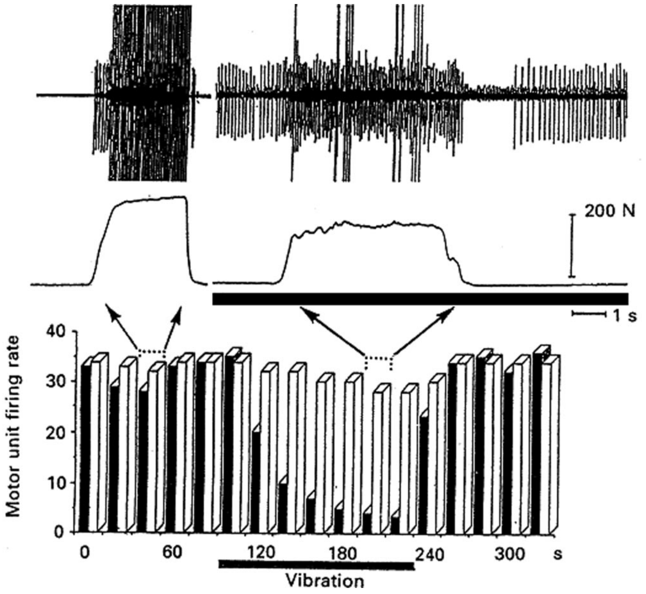

FIGURE 2—Reduction in MVC force and discharge rate of motor units in the tibialis anterior muscle due to prolonged vibration of the ankle flexor muscles. The bottom diagram shows the effect of prolonged vibration on the discharge rates of a high-threshold (*filled bars*) and a low-threshold motor unit (*open bars*) in recurrent brief MVCs. The upper recordings show on an expanded time scale the force developed and the discharges of the two motor units in one of the control MVCs and in one of the MVCs performed in the later part of the vibration period. (Reprinted from Bongiovanni et al. (2).)

In maximal contractions, however, precise discrimination of individual motor units is technically difficult, so the peak force and EMG amplitude are often used as windows to examine the activity of a pool of motor units. Further information on the effects of prolonged vibration (30 min) on the activity of motor unit pools is discussed below based on the studies on knee extensor (18) and ankle extensor (30) synergistic muscles.

Specific influence on vibrated muscle without alterations in voluntary drive.

In addition to reducing motor unit activity, prolonged tendon vibration (2) may also influence the excitability of the motor cortex (17) and the feedback transmitted by group Ib afferents (13). To assess the motor cortex excitability while ruling out the influence of Ib afferents, Kouzaki et al. (18) examined the effect of prolonged vibration applied to a single synergist on the capacity of other synergistic muscles during a maximal contraction. Vibration (30 Hz) was applied over the proximal portion of a relaxed rectus femoris muscle for 30 min. Before and after prolonged muscle vibration, subjects performed a maximal knee extension, and peak force and EMG amplitude across synergist muscles were assessed. The MVC force of the knee extensor muscles decreased by 10% (Fig. 3) was accompanied by similar decrease (14%) in the EMG amplitude of rectus femoris muscle, but not of the vastus lateralis or medialis muscles. These results are consistent with Jackson and Turner (15) after vibration of the rectus femoris muscle. The absence of a reduction in EMG amplitude in the nonvibrated, synergistic muscles suggests that voluntary drive for knee extension was not attenuated and that vibration of a single synergistic muscle does not

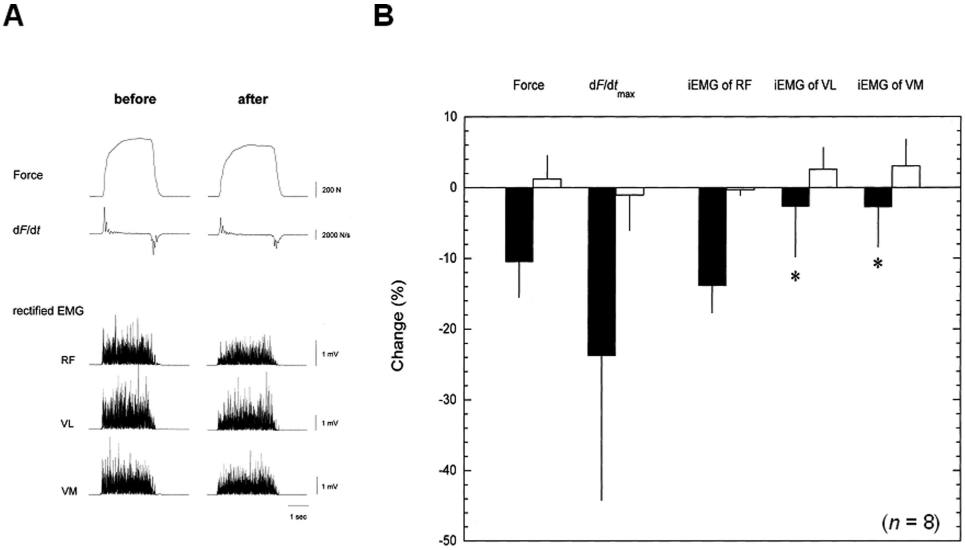

FIGURE 3—Effects of prolonged vibration of the rectus femoris muscle on peak force, rate of force development, and EMG amplitude in the knee extensor muscles during an MVC. A. Representative recordings for force, rate of force development (d*F*/d*t*), rectified EMG of rectus femoris (RF), vastus lateralis (VL), and vastus lateralis (VM) muscles during MVC before and after prolonged muscle vibration. B. Relative change in the peak force, maximal rate of force development (d*F*/d*t*max), and integrated EMG (iEMG) of RF, VL, and VM during MVC after prolonged muscle vibration (*filled bars*) and in the control experiment without vibration (*open bars*). * Significant difference ($P < 0.05$) compared with iEMG of RF. (Reprinted from Kouzaki et al. (18).)

influence the motor unit activity of other knee extensor synergistic muscles. Although there are limitations of using EMG amplitude as an index of central drive (10), an additional observation of the EMG burst strengthens this argument. The maximal rate of force development was decreased by prolonged vibration of the rectus femoris muscle due to depression of the large EMG burst in the rectus femoris muscle at the onset of the contraction. This finding may indicate an inability to activate high-threshold motor units with high initial discharge rates after prolonged vibration (2). Hence, prolonged vibration of a single synergistic knee extensor muscle results in a reduction in MVC force by the selective attenuation of Ia afferent input originating from the vibrated muscle.

Nonuniform responses in synergistic muscles. To assess the possibility that vibration applied to a common tendon may evoke variable responses among synergist muscles, Ushiyama et al. (30) examined the effect of prolonged tendon vibration on Hoffman reflex (H reflex) and EMG amplitude during a maximal contraction. The H reflex at rest was tested and subjects performed an ankle extension MVC before and after prolonged tendon vibration. Vibration (100 Hz) was applied to the Achilles tendon for 30 min while the muscles were relaxed. Although a tonic vibration reflex was not evoked, the amplitude of vibration (1.5 mm) was large enough to activate Ia afferents (0.2–0.5 mm) (23). The prolonged vibration decreased H reflex amplitude by a similar amount across the synergistic muscles (34–39%), which suggests that similar levels of presynaptic inhibition of Ia terminals (14) or transmitter depletion at Ia synapses (7) occurred in all the muscles. Although the MVC torque decreased by 17%, maximal twitch force evoked by supramaximal electrical stimulation did not change. Hence, the reduction in MVC torque would presumably be explained simply by a reduction in the excitatory Ia afferent input to the motor neuron pools of the ankle extensor muscles. The nonuniform effect on EMG amplitude, however, complicates this interpretation. The decrease in the MVC torque was accompanied by a reduction in amplitude of EMG in medial (13%) and lateral (11%) gastrocnemii muscles, but not in the soleus muscle. A similar decline in MVC force (19%) without a reduction in soleus EMG has been observed after prolonged tendon vibration in a separate study by Yoshitake et al. (31) as well.

The absence of a reduction in EMG amplitude of the soleus muscle may be due to enhanced sensitivity of the muscle spindle or decreased inhibitory input to the α motor neuron pool of the soleus muscle. There is no report, however, that suggests increased activation of γ motor neurons after prolonged vibration that enhances sensitivity of the muscle spindle during a maximal contraction. In addition, the discharge threshold of group Ia fibers increases after prolonged vibration (13), and there is little reason to assume that alteration in the sensitivity of the muscle spindle is unique in the soleus muscle compared with other ankle extensor muscles. Hence, enhanced sensitivity of the muscle spindle specific to the soleus muscle is unlikely after prolonged tendon vibration.

Potential inhibitory inputs to the α motor neurons that would be influenced by tendon vibration includes afferent inputs originating from the Golgi tendon organ and the muscle spindle via interneurons. Involvement of the afferent inputs from the Golgi tendon (Fig. 1) is unlikely because this potential effect should have been apparent uniformly across the ankle extensor muscles. Instead, the potential inhibitory input specific to the soleus muscle may involve Ia afferent input from the gastrocnemius medialis muscle via inhibitory interneurons (12,24). The reductions in the H reflex and EMG amplitude of gastrocnemii muscles indicate that excitatory Ia afferent input from gastrocnemii muscles to the homonymous motor neuron pool was reduced during a maximal contraction after prolonged vibration. This reduction must have accompanied decreased inhibitory Ia input to the α motor neuron pool in the soleus muscle as well. Hence, it is likely that decreased inhibitory Ia input from the gastrocnemius medialis muscle to the α motor neuron pool of the soleus muscle may compensate for the reduced excitatory Ia input from the soleus muscle, resulting in unaltered motor unit activity only in the soleus muscle during a maximal contraction.

Collectively, prolonged vibration does not impair voluntary drive, but reduces excitatory Ia afferent input, leading to a reduction in the activity of the motor unit pool in the vibrated muscles and MVC force. Although the reductions in excitatory Ia afferent input to the homonymous motor neuron pools are uniform across synergistic muscles, inhibitory neural connections may lead to a difference in motor unit activity across the synergistic muscles.

SUBMAXIMAL CONTRACTION

Force fluctuations during submaximal contractions are influenced by multiple features of the activation pattern in a pool of motor units (28). Hence, force fluctuations can be used as a window to evaluate the activation strategy of motor unit pools during steady contractions. Effects of prolonged vibration on force fluctuations have been examined during steady, submaximal contractions with the ankle extensor muscles (31) and a hand muscle (25).

Reduced force fluctuations after prolonged vibration without a tonic vibration reflex in leg muscles. Yoshitake et al. (31) examined whether prolonged tendon vibration of the ankle extensor muscles alters force fluctuations during submaximal steady contractions. Subjects matched their ankle extension force to a target ($\leq$10% MVC) as steady as possible before and after prolonged vibration. Prolonged vibration (100 Hz) was applied to the Achilles tendon for 30 min. A tonic vibration reflex was not evoked, but the amplitude of vibration (1.5 mm) was large enough to activate Ia afferents (23). Because the protocol for prolonged vibration was similar to the one in Ushiyama et al. (30), it was assumed that excitatory Ia afferent input to the α motor neuron pools was decreased during the prolonged vibration. In addition, it has been reported that depression of H reflexes induced by prolonged vibration lasts as long as 20 min (13,29,30).

Prolonged tendon vibration decreased the force fluctuations (SD) by 29% across target forces. Altered EMG activity across the ankle extensor synergists has been suggested to influence the force fluctuations (26), but there was no change in EMG amplitude across synergistic muscles in this study. Power spectral analysis of force further revealed that most of the power was $\leq$5 Hz with a peak $<$1 Hz, and significant reductions in power were limited to low-frequency bandwidths ($\leq$2 Hz) after prolonged vibration (Figs. 4 and 5). The low-frequency oscillation in force may be due to a common oscillation in the motor unit discharges (6). Furthermore, afferent input can modulate the oscillation of the membrane potential in the α motor neurons (21). Hence, it is possible that a reduction in the excitatory input from Ia afferents by prolonged vibration reduces force fluctuations presumably by modulating the low-frequency oscillation in the motor unit discharges. Further investigation is required to explore this potential mechanism.

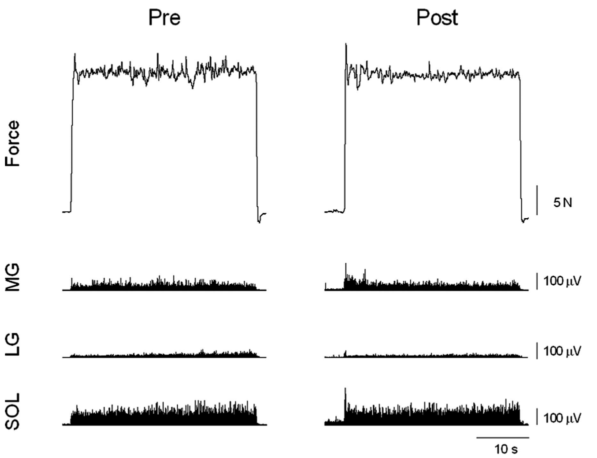

FIGURE 4—Representative recordings for ankle extension force and rectified EMG of medial gastrocnemius (MG), lateral gastrocnemius (LG), and soleus (SOL) muscles during steady contractions of ankle extensors before (Pre) and after (Post) prolonged tendon vibration. (Reprinted from Yoshitake et al. (31).)

Increased force fluctuations after prolonged vibration with a tonic vibration reflex in a hand muscle. Shinohara et al. (25) recently examined the influence of prolonged vibration of a hand muscle on the activity of Ia afferents and motor units. Subjects matched abduction force exerted by the index finger to a target force as steady as possible for 10 s, followed by quick stretches of the muscle while matching the same target force. Target force was 5.1% on average, which was 2.5% above the recruitment threshold of identified motor units. Subjects repeated this task before and after prolonged vibration (75 Hz), which was applied to the first dorsal interosseus muscle for 30 min. To ensure that vibration effectively influenced Ia afferents despite the small contact area (11-mm diameter) on the muscle, the location and amplitude of the vibration were ad-

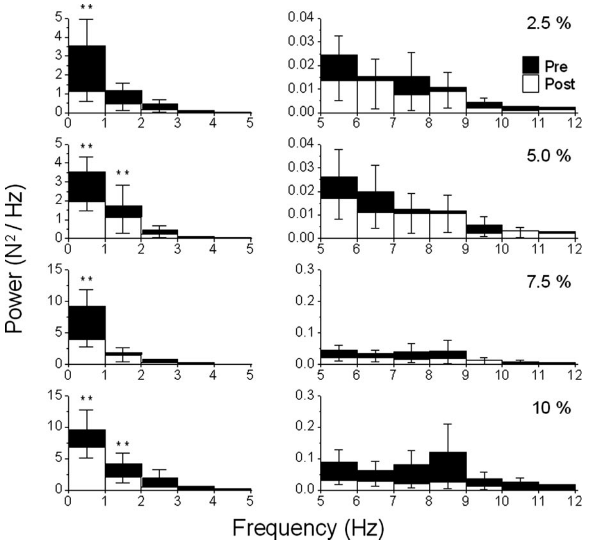

FIGURE 5—Power spectral density of force before and after prolonged tendon vibration at 4 targets (2.5–10% MVC). Data after vibration (Post, *open bars*) are superimposed with the data before vibration (Pre, *filled bars*). Note that the y-axis scales are different for below and above 5 Hz for visual purpose. ** $P < 0.01$ before and after vibration. (Reprinted from Yoshitake et al. (31).)

justed so that a tonic vibration reflex (<5% of maximal EMG amplitude) was induced.

Contrary to expectations, prolonged vibration increased the amplitude of the short-latency reflex, and it accompanied a slight increase in the background EMG. This observation implies that greater excitation of the α motor neuron pool was necessary to overcome impaired muscle contractility and/or heightened activity in the antagonist muscle (second palmar interosseus) after prolonged vibration. It is of note that a tonic vibration reflex was induced in this study. Although the maximal twitch force was unaffected after prolonged vibration without a tonic vibration reflex (30), a sustained tonic vibration reflex induced by prolonged vibration may induce a failure in the excitation-contraction coupling that is known to develop during prolonged low-force contractions (9). Indeed, the decline in the MVC force after prolonged vibration with a tonic vibration reflex (15%) was similar to that (15%) observed after a prolonged voluntary contraction (60 min) as low as 2.5% MVC (19). In support of the heightened activity in the antagonist muscle, 30-min vibration of the distal wrist flexor tendons enhanced corticospinal excitability in the antagonist muscle (extensor carpi radialis brevis) (27). The varying responses of the stretch reflex in the hand muscle and the H reflex in the leg muscles require further examination.

In this study (25), the amplitude of EMG and mean discharge rate of motor units in the first dorsal interosseus muscle increased significantly with no change in discharge rate variability, and the SD of force increased by 21% during steady contractions after prolonged vibration. The increase in the amplitude of EMG and mean discharge rate may be due to an increase in descending drive, which increases force fluctuations during constant force production. The association between the increase in motor unit activity and force fluctuations is consistent with observations of other interventions (26). In contrast, potential heightened activity in the antagonist muscle does not appear to influence the force fluctuations (5).

Collectively, prolonged vibration that does not evoke a tonic vibration reflex decreases the excitatory Ia afferent input to the α motor neuron pool, which helps to reduce the force fluctuations. In contrast, prolonged vibration that generates a tonic vibration reflex may reduce the Ia afferent input and increase the force fluctuations, probably due to an increase in descending drive.

CONCLUSIONS

Prolonged vibration does not impair the voluntary drive to muscle during maximal contractions, but reduces excitatory Ia afferent input that originates from the vibrated muscles, leading to a reduction in the MVC force due to an inability to maximally activate the motor units. Alterations in the activity of the motor unit pool could be variable across synergistic muscles due to potential neural connections between synergistic muscles. A vibration-induced reduction in Ia afferent input in leg muscles during steady, submaximal contractions decreases force fluctuations, possibly by reducing low-frequency modulation of motor unit discharge rate. When prolonged vibration that induces a tonic vibration reflex is applied to a hand muscle, the mean discharge rate of motor units increases, leading to increased force fluctuations during submaximal steady contractions.

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