Muscle dependency of corticomuscular coherence in upper and lower limb muscles and training-related alterations in ballet dancers and weightlifters

Junichi Ushiyama,1,2 Yuji Takahashi,2 and Junichi Ushiba1,3,4

1Department of Rehabilitation Medicine, Keio University School of Medicine, Tokyo; 2Graduate School of Science and Technology, Keio University, Kanagawa; 3Department of Biosciences and Informatics, Keio University, Kanagawa; and 4Keio University Tsukigase Rehabilitation Center, Shizuoka, Japan

Submitted 6 August 2009; accepted in final form 2 August 2010

Ushiyama J, Takahashi Y, Ushiba J. Muscle dependency of corticomuscular coherence in upper and lower limb muscles and training-related alterations in ballet dancers and weightlifters. J Appl Physiol 109: 1086–1095, 2010. First published August 5, 2010; doi:10.1152/japplphysiol.00869.2009.—It has been well documented that the 15- to 35-Hz oscillatory activity of the sensorimotor cortex shows coherence with the muscle activity during weak to moderate steady contraction. To investigate the muscle dependency of the corticomuscular coherence and its training-related alterations, we quantified the coherence between electroencephalogram (EEG) from the sensorimotor cortex and rectified electromyogram (EMG) from five upper limb (first dorsal interosseous, flexor carpi radialis, extensor carpi radialis, biceps brachii, triceps brachii) and four lower limb muscles (soleus, tibialis anterior, biceps femoris, rectus femoris), while maintaining a constant force level at 30% of maximal voluntary contractions. Five untrained subjects demonstrated the muscle dependency of corticomuscular coherence. The magnitude of the EEG-EMG coherence was significantly greater in the distally located lower limb muscles, such as the soleus and tibialis anterior, than in the upper or other lower limb muscles in untrained subjects (P < 0.05). These results imply that oscillatory coupling between the sensorimotor cortex and spinal motoneurons during steady contraction differs among muscles, according to the functional role of each muscle. In addition, the ballet dancers and weightlifters showed smaller EEG-EMG coherences than the untrained subjects, especially in the lower limb muscles (P < 0.05). These results indicate that oscillatory interaction between the sensorimotor cortex and spinal motoneurons can be changed by long-term specialized use of the muscles and that this neuronal adaptation may lead to finer control of muscle force during steady contraction.

Address for reprint requests and other correspondence: J. Ushiyama, Dept. of Rehabilitation Medicine, Keio Univ. School of Medicine, 35 Shinnanomachi, Shinjuku-ku, Tokyo 160-8582, Japan (e-mail: ushiyama@bme.bio.keio.ac.jp).

IT HAS BEEN well documented that the oscillatory activity of the sensorimotor cortex, measured by electroencephalogram (EEG) or magnetoencephalogram (MEG), shows coherence with the results of electromyogram (EMG) during weak to moderate steady contractions in both animals (4, 38) and humans (9, 21, 28, 35, 37, 52), with a peak frequency around 20 Hz. This corticomuscular coherence had been regarded as an efferent phenomenon, i.e., oscillations are propagated from the cortical source to the spinal motoneurons via the corticospinal tract. For example, Salenius et al. (52) demonstrated that MEG signals showed clear periodicity and always preceded EMG signals, dependent on the conduction distance between the cortex and the contracting muscle. However, several recent studies have implied that the mechanism of corticomuscular coherence may be more complex. Pohja and Salenius (46) demonstrated that ischemia-induced sensory deafferentation decreased the magnitude of corticomuscular coherence. In addition, Riddle and Baker (48) reported that changes in the phase of the corticomuscular coherence following arm cooling, which increased peripheral conduction time in both afferent and efferent nerves, was larger than that expected from the measured change in efferent conduction time. These results suggest that not only the motor cortex activity but also the peripheral feedback affect the oscillatory coupling between the sensorimotor cortex and the contracting muscle.

Furthermore, it is possible that, in addition to the above-mentioned anatomic characteristics, the muscle usage in daily living may modulate corticomuscular coherence. Indeed, recent studies (53, 54) have demonstrated that the motor unit coherence of the finger muscle was smaller in the dominant hand and was greater in weightlifters than in untrained subjects, but weaker in musicians. These findings suggest that long-term specialized use of the muscles induces adaptation of the strategy used by the central nervous system to perform a particular contraction. Based on these findings, if long-term muscle use changes the cortical control of the contracting muscle activity, we also hypothesized that training-related alterations in the corticomuscular coherence would be observed in the various muscles, depending on the types of habitual activity, i.e., skill- or strength-trained.

The present study tested these two hypotheses. First, we investigated the EEG-EMG coherence of various upper and lower limb muscles with different characteristics in normal (untrained) individuals, to confirm the muscle dependency of the oscillatory coupling between the sensorimotor cortex and the contracting muscles. Furthermore, in order to examine the...
effects of long-term muscle use on the control strategy for muscle contraction, we compared the EEG-EMG coherence in untrained individuals with that in skill-trained (ballet dancers) and strength-trained (weightlifters) individuals.

METHODS

Subjects. Forty-six healthy volunteers participated in this study. All subjects were right-handed and had no history of neurological disorders. The subjects were divided into three groups according to their sports experience as follows: 1) 24 untrained subjects (aged 21–31 yr; 12 male, 12 female) who had no specialized use of their limb muscles other than normal daily activities; 2) 12 female ballet dancers (aged 19–29 yr), who had regularly performed ballet for 6 h/wk for an average of 8 yr; 3) 10 male weightlifters (aged 19–22 yr), who had regularly performed resistance training for 10 h/wk for an average of 3 yr. All participants provided informed consent for the study after receiving a detailed explanation of the purpose and potential benefits and risks involved. The experimental procedures used in this study were approved by the local ethics committee of the Faculty of Science and Technology, Keio University.

EMG and EEG recordings. Bipolar surface EMG recordings were made from nine muscles in the right hand, arm, and leg, over the muscle bellies, using bipolar Ag/AgCl electrodes with a diameter of 5 mm and an interelectrode distance of 20 mm. The muscles used were the first dorsal interosseous (FDI), flexor carpi radialis (FCR), extensor carpi radialis (ECR), biceps brachii (BB), triceps brachii (TB), soleus (SOL), tibialis anterior (TA), biceps femoris (BF), and rectus femoris (RF).

Differential EEG recordings were made over the left sensorimotor cortex using a pair of Ag/AgCl surface electrodes with a diameter of 5 mm. Appropriate electrode position was determined according to the international 10–20 system of EEG electrode placement. The electrodes were placed at C3 and its 20-mm frontal position while the subjects contracted their upper limb muscles, and at Cz and its 20-mm left lateral position while the subjects contracted their lower limb muscles. The reference electrode was placed at A2 (right earlobe). An additional electrode was placed at A1 (left earlobe) as a ground electrode.

EEG and EMG signals were amplified using a custom-made amplifier designed by Thakor and Webster (60). The total gains of the EEG and EMG were 85 and 72 dB, respectively. All analog EEG and EMG signals were filtered using first-order bandpass filters (EEG, 4.8–80 Hz; EMG, 9.5–250 Hz) and were converted to digital signals at a sample frequency of 1 kHz with an input resolution of 16-bit via a data-acquisition card [ADA16–32/2(CB)F, Contec, Osaka, Japan]. The data-acquisition card was controlled by MATLAB software (The Math Works), and the digital data were stored on the hard disk of a personal computer.

Experimental protocol. Subjects were comfortably seated on a chair and performed tonic isometric contraction of each of nine muscles at 30% of maximal voluntary contraction (MVC) for 70 s. In the FDI task, the subjects abducted the right arm at ~30° and flexed the elbow to a right angle, with the hand and forearm pronated and resting on the desk. All digits were extended in the horizontal plane. The hand was secured to isolate FDI and restrict movement to all digits other than the index finger. In the FCR task, the subjects abducted the right arm at ~30° and flexed the elbow to a right angle, with the hand and forearm supinated and resting on the desk. In the ECR task, the subjects adopted an arm and elbow position similar to that during the FDI task. In the FCR and ECR tasks, the forearm was secured to restrict any elbow movement, and all digits were flexed. In the BB and TB tasks, the subjects flexed the shoulder at 90° and put their elbow on the desk with the elbow angle at 90°. The hand and forearm were supinated and all digits were flexed. Care was taken to restrict any wrist and shoulder movements. In the SOL and TA tasks, the subjects fixed the knee and ankle joints at 90° and 0° (neutral position), respectively. In the RF and BF tasks, the subjects adopted a posture similar to that during the SOL and TA tasks but suspended the leg from the ground. In all experiments involving the leg muscles, the thigh was secured to restrict any rotation.

Each subject performed MVCs before the experiment on each muscle. The subjects then watched the simple, unfiltered rectified EMG signals on a computer screen positioned in front of them and practiced to achieve EMG signals as close as possible to the line corresponding to 30% of the averaged amplitude of the rectified EMG for MVC. After sufficient practice, they performed a tonic isometric contraction at the same level for 70 s. The subjects repeated the same procedures with each of the nine muscles. The order of the muscles recorded was randomized among the subjects. A sufficient interval (at least 120 s) was given between each muscle contraction.

Data analysis. Data from the last 60 s were analyzed. EMG signals were rectified, as full wave rectification is known to provide the temporal pattern of grouped firing motor units (22). EEG and EMG signals were segmented into artifact-free epochs of 1,024 ms in duration, with no overlap (58 epochs). According to the methods of several previous studies (4, 15, 18), each 1024-ms data segment was Hanning-windowed to reduce spectral leakage. To estimate the correlation between the sensorimotor cortex and contracted muscle activities in the frequency domain, coherence values were calculated between EEG and rectified EMG signals using a fast Fourier transform algorithm with a frequency resolution, according to the following equation (22):

\[ |C_{xy}(f)|^2 = \frac{P_{xy}(f)^2}{P_{xx}(f) \cdot P_{yy}(f)} \tag{1} \]

where \( P_{xy}(f) \) and \( P_{xy}(f) \) are the averaged auto spectra of the EEG and the rectified EMG signals throughout the segments for a given frequency \( f \), respectively. \( P_{xy}(f) \) is the cross-spectrum between them throughout the segments. Coherence functions provide normative measures of linear correlation on a scale of 0 to 1, where 1 indicates a perfect linear correlation.

Coherence is considered to be significant if the resulting value exceeds the 95% confidence level (CL) (50). CL was defined as follows:

\[ CL(\alpha) = 1 - \left( 1 - \frac{\alpha}{100} \right)^{\frac{1}{n-1}} \tag{2} \]

where \( n \) is the number of epochs and \( \alpha \) is the P value (in %). In the present study, \( \alpha \) of 95% was chosen, resulting in the CL of 0.051.

According to Halliday et al. (22), timing information between EEG and EMG was calculated in the frequency and time domains. In the frequency domain, we estimated the phase spectrum, defined as the argument of cross-spectra. In the time domain, the cumulant density between EEG and EMG was estimated to characterize the correlation between the two signals.

Coherence was normalized by use of the arc hyperbolic tangent transformation for the latter statistical analysis (22). With respect to all data in which the EEG-EMG coherence curve exceeded CL, the maximal peaks of the coherence were observed in the 15- to 30-Hz range, as reported by many previous studies (4, 9, 21, 28, 35, 37, 38, 52). Thus, as data in which the EEG-EMG coherence curve exceeded CL, the maximal coherence curve (Cohmax) in the frequency range of 15–35 Hz (\( \beta \) band), and the frequency where Cohmax was observed (FP). We also calculated the frequency where the coherence curve first met CL when traced backward from FP (F1), and the frequency where the coherence curve first met CL when traced forward from FP (F2). We then estimated the area of the coherence curve in the frequency range of F1 and F2 (Coharea). When Cohmax was below CL, Coharea was estimated at 0.

Statistical analysis. Values are given as means ± SD. First, to confirm whether there are sex differences in Cohmax and Coharea.
not exceed CL across the entire frequency range (Cohmax = 0.048). We failed to observe any clear rhythmic or synchronous oscillations in EEG and EMG signals in this subject. These results indicate that, even though simple isometric contraction was performed using the same muscles, large differences in corticomuscular coherence existed among individuals.

As mentioned in METHODS, the maximal peaks of the EEG-EMG coherence were observed in the 15- to 35-Hz frequency range in all subjects and for all muscles, as reported in many previous studies (4, 9, 21, 28, 35, 37, 38, 52). Other distinct coherence peaks were occasionally noted at around 10 or 40 Hz, but these were smaller and less frequent than those observed in the 15- to 35-Hz frequency range. Subsequent examination of the oscillatory coupling between the sensorimotor cortex and the contracting muscle in this study therefore focused on the EEG-EMG coherence in the β band.

Examples of the PSDs for the EEG and rectified EMG signals, coherence spectra, phase spectra, and cumulant densities between the EEG and rectified EMG signals of each muscle in a representative untrained subject, ballet dancer, and weightlifter are shown in Fig. 3. The EEG-EMG coherence values clearly differed among muscles in the untrained subject, i.e., the coherence was larger in the distal lower limb muscles, such as the SOL and TA, than in the upper or other lower limb muscles. In the untrained subject, the peaks for EEG and EMG PSDs and the constant positive slopes of the phase spectra within the frequency range where the coherence curves exceed CL were much clearer in the SOL and TA than in other muscles. The corresponding EEG-EMG cumulant also showed a more prominent dip crossing time 0 in the SOL and TA than in the other muscles. Furthermore, the EEG-EMG coherence was larger in the untrained subject than in the ballet dancer or the weightlifter, especially in the lower limb muscles. For ballet dancers and weightlifters, we seldom found clear positive slopes of the phase spectra and significant cumulant density functions.

First, we analyzed whether there is a sex difference in the EEG-EMG coherence for the untrained subjects. As a result, ANOVA showed no significant sex differences in both Cohmax (F1,8 = 0.0024, P = 0.9616) and Coharea (F1,8 = 0.3813, P = 0.5495). Thus we confirmed that the effects of sex, and presumably body size, on the magnitude of EEG-EMG coherence were small in the present study. According to these results, we compared the data for the entire group of untrained subjects, including both sexes, with those of ballet dancers and weightlifters in the following analyses.

The group data (mean ± SD) for Cohmax (Fig. 4A) and Coharea (Fig. 4B) for all muscles and for all subject groups are shown. The effects of muscle (F8,16 = 6.07, P < 0.0001) and subject group (F2,16 = 6.48, P = 0.003) on Cohmax were highly significant. Similarly, the effects of muscle (F8,16 = 4.81, P < 0.0001) and subject group (F2,16 = 4.43, P = 0.018) on Coharea were also highly significant.

The significant interactions between muscles and subject groups in Cohmax (F16,728 = 3.08, P < 0.0001) and Coharea (F16,728 = 3.07, P < 0.0001), and the differences among the muscles for the three subject groups were therefore tested separately. The post hoc analysis showed that there were significant differences in EEG-EMG coherences among muscles in the untrained subjects. Cohmax of the SOL (0.201 ± 0.134) was significantly higher than that of the FDI (0.122 ±
0.065, \( P = 0.0021 \)), FCR (0.114 \pm 0.076, \( P = 0.0002 \)), ECR (0.116 \pm 0.059, \( P = 0.0001 \)), BB (0.077 \pm 0.043, \( P < 0.0001 \)), TB (0.101 \pm 0.036, \( P < 0.0001 \)), and RF (0.123 \pm 0.111, \( P = 0.0008 \)). Cohmax of the TA (0.228 \pm 0.155) was also higher than that of the FDI, FCR, ECR, BB, TB, RF (all, \( P < 0.0001 \)), and BF (0.143 \pm 0.097, \( P = 0.0095 \)). Cohmax of the SOL (0.895 \pm 1.224) was significantly larger than that of the FDI (0.308 \pm 0.268, \( P = 0.0153 \)), FCR (0.314 \pm 0.490, \( P = 0.0001 \)), ECR (0.316 \pm 0.312, \( P = 0.0017 \)), BB (0.126 \pm 0.154, \( P < 0.0001 \)), TB (0.184 \pm 0.129, \( P < 0.0001 \)), BF (0.424 \pm 0.493, \( P = 0.0279 \)) and RF (0.412 \pm 0.749, \( P = 0.0005 \)), but smaller than that of TA (1.341 \pm 1.673, \( P = 0.0176 \)). Cohmax of the TA was also larger than that of the FDI, FCR, ECR, BB, TB, BF, and RF (all, \( P < 0.0001 \)). No similar muscle-dependent differences in EEG-EMG coherence were observed in the ballet dancers or weightlifters.

Significant differences in EEG-EMG coherence among subject groups were detected for several muscles. Cohmax and Coharea of the SOL and TA were significantly higher in untrained subjects than in ballet dancers (SOL Cohmax, 0.086 \pm 0.042; TA Cohmax, 0.097 \pm 0.049; SOL Coharea, 0.152 \pm 0.1251; TA Coharea, 0.242 \pm 0.176; all, \( P < 0.0001 \)) and weightlifters (SOL Cohmax, 0.115 \pm 0.078, \( P = 0.0002 \); TA Cohmax, 0.100 \pm 0.059, \( P < 0.0001 \); SOL Coharea, 0.353 \pm 0.514, \( P = 0.0078 \); TA Coharea, 0.233 \pm 0.202, \( P < 0.0001 \)). In addition, Cohmax of the BF was significantly higher in the untrained subjects than in the ballet dancers (0.076 \pm 0.027, \( P = 0.0290 \)) and weightlifters (0.071 \pm 0.029, \( P = 0.0284 \)).

**DISCUSSION**

The main findings of the present study were that 1) the EEG-EMG coherence was greater in the distal lower limb muscles, such as the SOL and TA, than in the upper or other lower limb muscles in untrained subjects; and 2) the EEG-EMG coherence was smaller in the ballet dancers and weightlifters than in the untrained subjects, especially in the lower limb muscles. These findings support our hypotheses that the corticomuscular coherence differs among muscles and that long-term specialized use of the muscles changes the corticomuscular coherence.

Certain biological constraints could potentially be related to the observed variations in EEG-EMG coherence among muscles and among subjects. The electrical field measured by EEG depends on several factors, including the direction of electrical current flow, which is affected by the orientation of the corticospinal neurons relative to the electrodes, the depth of the corticospinal neurons relative to the scalp, and the thicknesses of the scalp and skull. These factors are likely to vary among different muscles and different subjects, and interpretation of the observed variations in the magnitude of EEG-EMG coherence among muscles or subjects assumes that the activity of the relevant cortical neurons was not successfully recorded by EEG electrodes in some cases because of these factors.

Regarding the effects of orientation of the neurons on EEG signals, some recent studies reported that, although distribution of the electric field differs depending on the direction of the current dipole, EEG can detect both radially and tangentially...
oriented sources, while MEG detects only sources oriented tangentially to the head (34, 41, 42, 63). Coherence is a measure of the linear correlation between two signals in the frequency domain and is defined as the cross spectra normalized by the auto spectra (22); thus coherence does not depend on the respective amplitudes of two signals but on the ratio between the amplitudes, and the degree of locking of the phase difference between them (27, 57). It is therefore reasonable to

Fig. 3. Typical examples of PSDs for EEG signals and rectified EMG signals, coherence spectra, phase spectra, and cumulant densities between EEG and rectified EMG signals in the first dorsal interosseous (FDI), flexor carpi radialis (FCR), extensor carpi radialis (ECR), biceps brachii (BB), triceps brachii (TB), soleus (SOL), tibialis anterior (TA), biceps femoris (BF), and rectus femoris (RF). Black lines, gray lines, and dotted lines represent the data for one untrained subject, ballet dancer, and weightlifter, respectively. Note that the phase spectra are only shown for the frequency range where the coherence curves exceeded CL. Thus, for data in which the coherence curve did not exceed CL or exceeded CL only at one point, we could not show the phase spectra.
assume that the orientation of the neurons is not a major contributory factor in the observed variations in EEG-EMG coherence among muscles or among subjects, although it does influence the EEG amplitude.

It is possible that the EEG electrodes would be unable to detect the relevant cortical activity if the population of cortical neurons was deeply located (e.g., the neurons in the foot-representation area), resulting in absent or reduced EEG-EMG coherence. However, the results of present study demonstrated that lower limb muscles, such as the SOL and TA, with neurons located deep in the cerebral sulcus, showed the greatest EEG-EMG coherence. This suggests that the motor-related cortical activity recorded by the EEG electrodes in the present study could be used to calculate EEG-EMG coherence, even when the populations of cortical neurons were located far from the recording site. This assumption is supported by previous studies, which found that movement-related cortical potentials were generally identified from EEG signals in the primary motor cortex, not only during voluntary hand movement (55, 58), but also during foot movement, with an amplitude of several to 10 μV (56, 59).

Furthermore, it has been documented that EEG is affected by the low-pass filter characteristics of the skull and scalp (19). Thus the amplitude of EEG signals may differ among subjects due to individual variations in the thicknesses of the skull and scalp. However, as mentioned above, coherence does not depend on the respective amplitudes of the recorded signals, and the effects of individual variations in skull and scalp thicknesses on the present results would therefore be limited.

Based on the physiological and theoretical points of view, we empirically assumed that the effects on the present results of variations in biological factors such as the location and orientation of relevant corticospinal neurons, and the thicknesses of the scalp and skull among subjects or among...
muscles were limited. However, we were unable to quantify the extent to which these factors might have influenced the results, because no studies have quantitatively examined the effects of these factors on the magnitude of EEG-EMG coherence. However, many studies have examined differences in corticomuscular coherence among muscles (7, 18, 19, 28, 36, 48), and among subject groups, i.e., between normal individuals and patients (14, 15, 19, 29, 40, 51), between karate athletes and nonathletes (61), and between adults and children (17, 25). Thus, although we cannot completely exclude the possibility that the above-mentioned biological factors might have influenced the results of the present study, the study design, i.e., comparing the magnitude of EEG-EMG coherence between muscles and between subject groups, represents an acceptable means of studying corticomuscular coherence, and the physiological mechanisms behind the results remain worthy of discussion.

Muscle dependency of the corticomuscular coherence. The data for the untrained subjects revealed differences in the magnitude of the EEG-EMG coherence between the upper and lower limb muscles, and between the proximal and distal muscles, particularly within the lower limb muscles. Although post hoc analyses failed to show any significant differences, a similar proximal-distal difference was also observed within the upper limb muscles. Furthermore, individual variations in the magnitude of the EEG-EMG coherence were observed, especially in the distally located lower limb muscles. The simplest interpretation of the observed variations in EEG-EMG coherence is that the relative contribution of the descending command to the excitatory spinal motoneurons differs among subjects and among muscles. However, it is also possible that the magnitude of the EEG-EMG coherence is influenced by the tendency of the cortical neurons to discharge in synchrony (33), i.e., a smaller magnitude of EEG-EMG coherence indicates that the discharge frequency of the cortical neurons is more variable and not synchronized, and that these neuronal behaviors, which do not contribute to the generation of EEG signals, generate nonoscillatory EMG activity. It is therefore likely that differences in the tendency of the corticospinal cell population to discharge in synchrony could also account for the observed variations in the magnitude of the EEG-EMG coherence among subjects and among muscles.

It is quite possible that observed muscle dependency of EEG-EMG coherence is related to the variability of the functional role of each muscle. Indeed, it has been well documented that the innervation ratio, i.e., different numbers of muscle fibers innervated by one motoneuron, varies among muscles. It is believed that the innervation ratio is roughly proportional to the size of the muscles and determines the functional muscle features, i.e., muscles with a lower innervation ratio, such as the hand or arm muscles, are suitable for fine motor control, whereas muscles with a higher innervation ratio, such as the leg muscles, are suitable for higher force production (16). It has also been suggested that proximal-distal differences in functional muscle features exist, even within each limb, such that the distal muscles mainly serve to control manipulative movements, while the proximal muscles control postural adjustment (24). Thus proximally located upper limb muscles are supposed to be more suited to constant force production, as in the task used in the present study. In the present study, the proximally located upper limb muscles, such as the BB and TB, showed the smallest EEG-EMG coherence, whereas the distally located lower limb muscles, such as the TA and SOL, showed the greatest EEG-EMG coherence. Therefore, the present results suggest that the observed muscle dependency of EEG-EMG coherence is related to variations in functional roles among muscles.

In terms of mechanisms involved in the observed proximal-distal differences in the EEG-EMG coherence, several anatomic factors can be proposed. It has been shown that the corticomotoneuronal cells exert more frequent and more potent terminations in the motoneuron pools of distal muscles than of proximal muscles, in both the upper (43) and lower limbs (5) in humans. Indeed, Kim et al. (30) demonstrated that motor unit coherence in the 15- to 40-Hz frequency range are more prevalent in distal muscles than in proximal muscles during steady contraction, suggesting that stronger corticospinal projections to muscles generate the prominent local rhythmic activity in distal muscles. Since the distal muscles showed larger EEG-EMG coherence in the present study, the density of the corticospinal projection might be one of the factors that determine the magnitude of corticomuscular coherence.

Additional factors may also be related to the observed proximal-distal differences in the EEG-EMG coherence. Renshaw cells are known to receive excitatory input from motoneurons and feedback inhibition to the same motoneuron pool (47). It has been demonstrated that this homonymous recurrent inhibition via Renshaw cells is weaker in distal muscles than in proximal muscles, in upper (23, 26) and lower limb muscles (49). Furthermore, a recent computational modeling study by Williams and Baker (62) showed that Renshaw cell inhibitory feedback reduces the corticomuscular coherence at both 10 Hz and 20 Hz, and then improves physiological tremor. Since these previous findings are consistent with the present results that the distal muscles showed larger EEG-EMG coherence both in upper and lower limb muscles, it can be assumed that the difference in the distribution of recurrent inhibition also contributes to the proximal-distal differences in the corticomuscular coherence.

Furthermore, muscle spindles are more abundant in distal muscles than in proximal muscles, especially in the lower limb muscles, i.e., the density of muscle spindles is reportedly higher in the SOL and TA than in the BF and RF (2). Baker et al. (3) recently demonstrated that spiking of primary (Ia) afferent nerves was coherent with oscillatory EMG activity over a wide frequency range, including the β-band (around 20 Hz), during isometric contraction. Thus Ia afferent signals seem to be related to the generation and/or modulation of oscillatory EMG activity in the β-band. Furthermore, Pohja and Salenius (46) reported a decrease in corticomuscular coherence due to ischemia-induced deafferentation. Based on these previous findings, it is reasonable to assume that Ia afferent signals return to the central nervous system from the muscle and contribute to the generation and/or modulation of corticomuscular coherence. It is possible that the more abundant number of muscle spindles within the muscle, the more strongly the Ia afferent signals are delivered to the sensorimotor cortex via the spinal cord. Thus it is suggested that the difference in the density of muscle spindles among muscles is also responsible for the proximal-distal differences in the magnitude of corticomuscular coherence.

Although the anatomic factors mentioned above could account for the proximal-distal differences in the EEG-EMG coherence, the mechanism involved in the difference in the
EEG-EMG coherence between the upper and lower limb muscles is still unclear. Indeed, it has been well documented that the corticospinal projections to the motoneurons are less dense in lower limb muscles than in upper limb muscles (5, 6), although the present results demonstrated greater EEG-EMG coherence in the lower limb muscles than in the upper limb muscles. Furthermore, according to several previous studies (2, 31, 44), muscle spindles are no more abundant in lower limb muscles than in upper limb muscles. The difference in EEG-EMG coherence between the upper and lower limb muscles cannot, therefore, be explained by these anatomic factors and is likely to be the result of acquired factors, such as differences in muscle usage during daily living activities. A lower observed EEG-EMG coherence in the upper limb muscles would be an example of central nervous system adaptation accompanied by a lifetime of training to promote more accurate force control. To examine the effects of specialized muscle use on the oscillatory coupling between the sensorimotor cortex and contracting muscles in more detail, we examined the difference in the magnitude of the EEG-EMG coherence between untrained and well-trained individuals (ballet dancers and weightlifters).

Training-related alterations in corticomuscular coherence. It is not known if the variability in corticomuscular coherence among individuals is determined by innate or acquired factors. Regarding neural adaptation induced by training,Semmler et al. (54) reported that the strength of coherence between pairs of motor units in the FDI, showing a peak at 10–30 Hz, was smaller in the right hand than in the left of right-handed untrained subjects, and much smaller in both hands of musicians, than in the left hand of untrained subjects, suggesting that the contribution of common oscillatory inputs, originating predominantly from the sensorimotor cortex, to perform sustained steady contraction was reduced by long-term specialized use of the muscle. Indeed, the present study also revealed training-related alterations in EEG-EMG coherence during sustained isometric contraction. The EEG-EMG coherence was significantly smaller in the ballet dancers and weightlifters than in the untrained subjects, especially in the lower limb muscles. The variability in EEG-EMG coherence among individuals was also smaller in the ballet dancers and weightlifters. Although we cannot deny the possibility that the corticomuscular coherence was inherently lower in some of the ballet dancers and weightlifters, the present statistical results imply that the oscillatory interaction between the sensorimotor cortex and the contracting muscles can be changed by acquired factors, i.e., by long-term specialized use of the muscles.

We should consider the functional significance of the training-related reductions in EEG-EMG coherence observed in the present study. Halliday et al. (20) demonstrated that the surface EMG activity showed coherence with the physiological tremor signal not only in the frequency range of 1–12 Hz but also of 15–30 Hz, and it can therefore be assumed that the magnitude of the oscillatory muscle activity in this frequency range is related to the motor performance of postural tasks. Although it has been generally documented that the 15- to 30-Hz component of the physiological tremor is smaller in amplitude than the lower frequency component (11), the present study revealed that the subjects with greater EEG-EMG coherence showed prominent oscillatory fluctuations in EMG signals at around 20 Hz, while the ballet dancers and weightlifters did not show such prominent oscillations in EMG signals in either their upper or lower limb muscles. Thus our data indicate that it is important to reduce corticomuscular coherence and then reduce such oscillatory muscle activity in order to stabilize the force fluctuation, and that habitual training in both ballet dancers and weightlifters appears to suppress the oscillatory coupling between the sensorimotor cortex and the spinal motoneurons, at least during simple sustained steady contraction in both the upper and lower limb muscles.

We defined ballet dancers as skill-trained subjects and weightlifters as strength-trained subjects and expected a difference in the magnitude of EEG-EMG coherence between these two groups. However, ballet dancers and weightlifters both showed smaller EEG-EMG coherences than the untrained subjects. This surprising result might be due to the similarity of the daily training between ballet dance and weightlifting. According to Nielsen et al. (39), ballet dancing is classed as anaerobic exercise, as is weightlifting. In addition, according to Enoka (12, 13), who demonstrated the joint power output about the hip, knee, and ankle joints during weightlifting events, the ability to successfully execute the weightlifting events depends on an athlete’s ability to organize the phases of power production and absorption into an appropriate temporal sequence. Thus it can be assumed that, especially for lower limb muscles, both sports require the coordinative control of many muscle activities to perform multiple movements with fine postural adjustments depending on an appropriate temporal sequence, and these similarities in daily training provide similar adaptations in corticomuscular coherence.

Our observation appeared to be at variance with the recent study by Perez et al. (45). Indeed, Perez et al. (45) demonstrated a significant increase in EEG-EMG coherence within the β-band after visuomotor skill learning, whereas our study revealed that trained subjects showed smaller EEG-EMG coherence at around 20 Hz. Several recent studies have demonstrated that the EEG-EMG coherence between different cortical regions increased in the early stage of skill learning with improved motor performance, and then decreased after learning (1, 8, 10, 32), suggesting that the greater initial functional coupling between distinct brain areas corresponds to the greater command integration when physiological processes are not yet safely established as motor routine, and that the system becomes more efficient after skill acquisition. If training-related changes in the corticospinal coupling are also due to the stage of motor learning, we can propose that the differences in the results between the study of Perez et al. (45) and the present study are due to the difference in the term of the training. Indeed, Perez et al. (45) investigated short-term active adaptation following 32 min of visuomotor training on EEG-EMG coherence, while this study showed chronic adaptation of the corticospinal coupling by comparing the magnitude of EEG-EMG coherence during steady contraction among different subject groups.

Since Semmler et al. (54) reported that the magnitude of motor unit coherence in FDI was higher in weightlifters than in untrained subjects, one might also expect that EEG-EMG coherence is also higher in weightlifters than in untrained subjects. However, the present study revealed that the magnitude of EEG-EMG coherence is smaller in the weightlifters than in the untrained subjects. First, we would like to emphasize that the significant differences in the magnitude of the EEG-EMG coherence between subject groups were observed in the lower limb muscles, not in the upper limb muscles. In addition, although it has been reported that motor unit coherence at around 20 Hz is at least partially responsible for the oscillatory activity from the sensorimotor cortex in literature (54), motor unit coherence could be influenced by other common
oscillatory inputs at the spinal level. Indeed, the muscle dependency of the motor unit coherence, as reported by Kim et al. (30), showed different tendencies from those of EEG-EMG coherence observed in this study, i.e., although motor unit coherence also showed proximal-distal differences in the upper and lower limb muscles, it is stronger in the upper limb muscles than in the lower limb muscles. Therefore, a possible explanation for the differences in the results between Semmler et al. (54) and the present study is that EEG-EMG coherence is, strictly speaking, a different measure from motor unit coherence.

Conclusions. The present data from untrained subjects demonstrated the muscle dependency of corticomuscular coherence, i.e., the EEG-EMG coherence was significantly greater in the lower limb muscles than in the upper limb muscles, and was greater in the distal muscles than in the proximal muscles. These results imply that oscillatory coupling between the sensorimotor cortex and the spinal motoneurons during sustained steady contraction differs among muscles, according to the functional role of each muscle. The present study also demonstrated that the EEG-EMG coherence was smaller in the ballet dancers and weightlifters than in the untrained subjects, especially in the lower limb muscles. These training-related alterations in corticomuscular coherence suggest that the oscillatory interaction between the sensorimotor cortex and the contracting muscles can be changed by long-term specialized use of the muscles and that this neural adaptation may lead to finer control of the muscle force during steady contraction.

GRANTS

The present study was partly supported by a Grant-in-Aid for Young Scientists (B) (No. 21700594) from the Ministry of Education, Culture, Sports, Science, and Technology (MEXT), Japan, by Keio Academic Development Funds, and by the Strategic Research Program for Brain Sciences (SRPBS) from MEXT, Japan.

DISCLOSURES

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

REFERENCES


