Contraction level-related modulation of corticomuscular coherence differs between the tibialis anterior and soleus muscles in humans

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Ushiyama J, Masakado Y, Fujiwara T, Tsuji T, Hase K, Kimura A, Liu M, Ushiba J. Contraction level-related modulation of cortico-muscular coherence differs between the tibialis anterior and soleus muscles in humans. J Appl Physiol 112: 1258–1267, 2012. First published February 2, 2012; doi:10.1152/japplphysiol.01291.2011.—The sensorimotor cortex activity measured by scalp EEG shows coherence with electromyogram (EMG) activity within the 15- to 35-Hz frequency band (β-band) during weak to moderate intensity of isometric voluntary contraction. This coupling is known to change its frequency band to the 35- to 60-Hz band (γ-band) during strong contraction. This study aimed to examine whether such contraction level-related modulation of corticomuscular coupling differs between muscles with different muscle compositions and functions. In 11 healthy young adults, we quantified the coherence between EEG over the sensorimotor cortex and rectified EMG during tonic isometric voluntary contraction at 10–70% of maximal voluntary contraction of the tibialis anterior (TA) and soleus (SOL) muscles, respectively. In the TA, the EEG-EMG coherence shifted from the β-band to the γ-band with increasing contraction level. Indeed, the magnitude of β-band EEG-EMG coherence was significantly decreased, whereas that of γ-band coherence was significantly increased, when the contraction level was above 60% of maximal voluntary contraction. In contrast to the TA, the SOL showed no such frequency changes of EEG-EMG coherence with alterations in the contraction levels. In other words, the maximal peak of EEG-EMG coherence in the SOL existed within the β-band, irrespective of the contraction levels. These findings suggest that the central nervous system regulates the frequency of corticomuscular coupling to exert the desired levels of muscle force and, notably, that the applicable rhythmicity of the coupling for performing strong contractions differs between muscles, depending on the physiological muscle compositions and functions of the contracting muscle.

electroencephalogram-electromyogram coherence; sensorimotor cortex; Piper rhythm

DURING WEAK TO MODERATE INTENSITY OF ISOMETRIC VOLUNTARY CONTRACTION, oscillatory neural activity of the sensorimotor cortex measured by EEG or magnetoencephalogram (MEG) shows coherence with electromyogram (EMG) activity in contralateral limb muscles within the 15- to 35-Hz frequency band (β-band) in humans (14, 15, 18, 25, 26, 34, 44, 58). Although this corticomuscular coherence was initially assumed to be an effenter phenomenon (5, 8, 18, 34), it was recently suggested that this coupling is mediated by not only motor pathways, but also somatosensory pathways, and reflects the sensorimotor integration processes (1, 40, 42, 57).

During strong intensity of isometric voluntary contraction, human muscle manifests a further tendency toward rhythmic oscillations at a higher frequency (35–60 Hz; γ-band). This muscle activation pattern was first denoted by Hans Piper in the EMG signal of strongly contracting muscle and is, therefore, designated the “Piper rhythm” (5, 16). A previous study found that microneurographic recording of spindle afferent nerves revealed no such rhythmic behavior correlated with the EMG Piper rhythm during strong contraction, suggesting that the EMG rhythm may originate centrally (16). In addition, some earlier studies demonstrated significant γ-band coherence between the EEG/MEG and EMG of strongly contracting muscle, by replacing the β-band coherence (5, 33). These findings suggest that the γ-band rhythmic drive from the cortex contributes to the increment in firing frequency of activated motor units at the population level and generates the EMG Piper rhythm, making it feasible to exert high-intensity muscle force.

To change the exerted muscle force levels, motor units are activated in two ways: namely, changing the number of activated motor units (recruitment/derecruitment), and modulating the firing frequency of the activated motor units (change in firing rate). The relative contributions of these two processes are known to vary between muscles, depending on differences in the muscle compositions, such as muscle size and/or fiber-type composition and functions (4, 10, 12, 27). In addition, it is known that the firing frequencies of activated motor units observed during strong contraction differ between muscles (4, 10, 12, 27). Considering such differences in the motor unit activation strategies between muscles, it is possible that the frequency of the grouped discharge observed in the EMG of strongly contracting muscle differs between muscles, depending on the muscle composition and function of the muscles. If so, this raises the question of whether frequency shifts of corticomuscular coherence from the β-band to the γ-band, depending on the muscle contraction levels, are generally observed in skeletal limb muscles. As is the case for muscles that maintain the firing rate of their motor units at lower frequencies, even during strong contraction, it is hypothesized that the frequency band of corticomuscular coherence does not change with changes in contraction level, or even if the frequency shift does occur, its variation range would be less than that of muscles with a higher firing rate of the activated motor units under high-intensity contraction.
To test this hypothesis, we measured the EEG-EMG coherence during weak, moderate, and strong intensities of isometric voluntary contractions of the tibialis anterior muscle (TA) and soleus muscle (SOL). The TA and SOL are the best-suited muscles to test this hypothesis for the following reasons: 1) distally located lower limb muscles, including the TA and SOL, show the greatest magnitude of EEG-EMG coherence among various upper and lower limb muscles, as our laboratory previously reported (51); 2) the discharge frequencies of motor units under high-intensity contraction are totally different between the TA (25–65 Hz) (7, 21, 53) and SOL (5–25 Hz) (4, 39); and 3) they are flat, straight, superficial muscles, making them amenable to surface EMG recording.

**Materials and Methods**

**Subjects**

Eleven healthy individuals (aged 22–31 yr; eight men and three women) participated in this study. All of the participants provided informed consent for the study after receiving a detailed explanation of the purpose, 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.

**EEG, EMG, and Force Recordings**

EEG recordings were made from the scalp near the sensorimotor cortex using five Ag-AgCl surface electrodes with a diameter of 10 mm, placed at Cz (defined by the international 10–20 system), and its 20-mm front, back, left lateral, and right lateral positions. The reference electrode was placed at A2 (right earlobe). An additional electrode was placed at A1 (left earlobe) as a ground electrode. EEG signals were derived using the Hjorth transformation (22). Surface EMG recordings were made from the TA and SOL, over the muscle belly, using bipolar Ag-AgCl electrodes with a diameter of 10 mm and an interelectrode distance of 20 mm. The impedance of the EEG and EMG electrodes was kept below 5 and 20 kΩ, respectively, during the recording.

All EEG and EMG signals were amplified and band-pass filtered (EEG, 0.5–100 Hz; EMG, 1–500 Hz) using a standard EEG and EMG recording system (Neurpack MEB-4308; Nihon Kohden, Tokyo, Japan). Force signals were recorded with force transducers (TU-BR; Nihon Kohden, Tokyo, Japan). All analog signals were converted to digital signals at a sample frequency of 1 kHz by an analog-to-digital converter with 12-bit resolution (NI-6071E; National Instruments, Austin, TX), controlled by data logger software originally designed using MATLAB software (The Mathworks, Natick, MA). Digital data were stored on the hard disk of a personal computer.

**Experimental Procedures**

The subjects were comfortably seated on a chair in a semireclining position. The right leg was fixed with the knee flexed at 90° and the ankle at 0° (neutral position). The foot was strapped to a plate to which a force transducer was attached, and the thigh was also secured to restrict any rotation.

Before the experiments on each muscle, the subjects performed an isometric dorsiflexion/plantar flexion, with maximal effort lasting ~3 s. Each maximal voluntary contraction (MVC) force was determined as a peak value of exerted force over the period of stable force output. After a sufficient rest period of ~120 s, the subjects separately performed tonic isometric voluntary dorsiflexion/plantar flexion at 10, 20, 30, 40, 50, 60, and 70% of MVC. Since muscle fatigue caused by prolonged contraction may induce acute changes in the magnitude of EEG-EMG coherence (48, 49), the trials at 10–40% of MVC were limited to periods of 12 s and were repeated five times. Since stronger contraction should easily induce muscle fatigue, the trials at 50–70% of MVC were limited to periods of 6 s and were repeated 10 times. A sufficient interval (at least 120 s) was given between each muscle contraction. The exerted force signal was visually fed back to a level meter on the computer screen positioned 1.2 m in front of the subjects. The subjects were instructed to maintain their exerted force as close as possible to the line corresponding to the target force level. When the subjects performed the tasks, the examiners checked that no EMG activity occurred in the antagonistic muscle. If antagonist EMG occurred, we omitted the data and allowed the subjects to perform the same trial again. The orders of the recorded muscles and contraction levels were randomized among the subjects.

**Data Analysis**

The EMG signals were rectified, because full-wave rectification is known to provide the temporal pattern of grouped firing of motor units (19, 20). Data from intermediate periods of 10.24 s (at 10–40% of MVC) and 5.12 s (at 50–70% of MVC) in each trial were used in the following analyses. The EEG and EMG data for each trial were segmented into several artifact-free epochs of 1,024 ms duration with no overlaps. All data segments were then gathered throughout the trials in the same task (same muscle and same contraction level) to provide 51.2 s of data (1,024 ms × 50 segments). Each 1,024-ms data segment was Hanning-windowed to reduce spectral leakage. The correlations between EEG and rectified EMG [C_{xy}(f)] were calculated by coherence using the following equation (20):

$$\left| C_{xy}(f) \right| = \frac{\left| P_{xy}(f) \right|^2}{P_{xx}(f) \cdot P_{yy}(f)}$$

where $P_{xx}(f)$ and $P_{yy}(f)$ are the averaged power spectral densities (PSDs) of the EEG and rectified EMG signals throughout the segments for a given frequency $f$, respectively, and $P_{xy}(f)$ is the averaged cross-spectral density between these two parameters throughout the segments.

The coherence function provides a normative measure of the linear correlation on a scale of 0 to 1, where 1 indicates a perfect linear correlation.

![Fig. 1. Coherence spectrum between the EEG over the sensorimotor cortex and rectified electromyogram (EMG) of the contracting muscles during sustained contraction at 40% of maximal voluntary contraction (MVC) of the tibialis anterior (TA) muscle. We calculated the maximal peaks of EEG-EMG coherence in the frequency ranges of 15–35 Hz (Coh x-max) and 36–65 Hz (Coh y-max). The estimated significance level (SL) of $P < 0.05$ is shown as a horizontal dashed line. See MATERIALS AND METHODS for more details.](http://jap.physiology.org/Downloadedfrom10.1152/japplphysiol.01291.2011 www.jappl.org)
To quantitatively evaluate the contraction level-related changes in the magnitude of β-band and γ-band EEG-EMG coherence, we set the frequency range for the latter analyses at 3–60 Hz (including the α-band, β-band, and γ-band). As shown in Fig. 1, we calculated the peak values of coherence within the 15- to 35-Hz band (Cohβ-max) and 36- to 60-Hz band (Cohγ-max), respectively. We also calculated the averaged coherence values within the 15- to 35-Hz band and the 36- to 60-Hz band to check the plausibility of the peak coherence analyses. As the modulation patterns of β- and γ-band averaged coherence were almost identical to the results using peak coherence, we only reported the results of Cohβ-max and Cohγ-max in the present study for the sake of brevity of the paper.

Additionally, to quantify the contraction level-related changes in EEG PSD for both the TA and SOL, we determined the ratio of the sum of PSD within the β-band or γ-band to that of the entire frequency range for EEG (EEG-βPSD and EEG-γPSD, respectively).

Statistical Analysis

For multiple comparisons across the 59 frequency bins (i.e., between 3 and 60 Hz), we applied a Bonferroni correction to the equation defining the significance level of coherence (SL) (20, 43). Thus, when the confidence limit is α%, the SL is estimated as follows (25, 49, 50):

\[
SL(\alpha) = 1 - \left[ \frac{1}{N} \left( 1 - \frac{\alpha}{100} \right) \right]^{1/(L-1)}
\]

where \(N\) is the number of frequency bins, and \(L\) is the number of epochs. As an \(N\) of 59, \(L\) of 50, and \(\alpha\) of 95 were chosen, the SL was determined to be 0.134 in the present study. This revision eliminates the potential risk that the coherence value is judged to be significant owing to a statistical error.

RESULTS

Figure 2 illustrates typical recordings of raw EEG and EMG signals, PSDs for EEG and rectified EMG, and coherence spectra between EEG and rectified EMG signals during tonic isometric voluntary contraction at 10% (weak), 40% (moderate), and 70% (strong) of MVC for the TA and SOL. For the TA, when performing weak contraction, β-band oscillations were clearly observed in both the EEG and EMG signals. Both the EEG and EMG PSDs showed distinct peaks in the β-band, and the maximal peak of EEG-EMG coherence occurred in the same frequency band. When performing moderate contraction, β-band oscillations were clearly observed in both the EEG and EMG signals. Both the EEG and EMG PSDs showed distinct peaks in the β-band and γ-band. During strong contraction, the γ-band components of the EEG and EMG PSDs became more prominent. The significant coherence peak within the β-band disappeared, and the peak of EEG-EMG coherence occurred within the γ-band. By contrast, for the SOL, β-band oscillatory activities were clearly observed in the raw EEG and EMG signals for all three contraction levels.
contraction levels. Indeed, prominent peaks for both the EEG and EMG PSDs existed within the β-band for all three contraction levels. In contrast to the TA, less clear peaks were observed within the γ-band in the EEG and EMG PSDs during strong contraction. Furthermore, the peaks of EEG-EMG coherence remained within the β-band, irrespective of the contraction levels.

Figure 3 shows the means ± SDs for EEG-β-PSD (Fig. 3A) and EEG-γ-PSD (Fig. 3B) at all contraction levels for both the TA and SOL. Note that these measures are the ratios of the sum of EEG PSD within the β-band (EEG-β-PSD) and γ-band (EEG-γ-PSD) to that of the entire frequency range, respectively. ANOVA revealed significant differences in EEG-β-PSD between the muscles (F_{1,10} = 10.443, P = 0.009) and contraction levels (F_{6,60} = 4.466, P = 0.001), but there was no significant interaction between muscle and contraction level (F_{6,60} = 1.924, P = 0.092). Thus, the differences in EEG-β-PSD among the contraction levels were tested for each muscle separately. In the TA, compared with the value at 10% of MVC (0.320 ± 0.141), significant decreases in EEG-β-PSD were detected at 50% (0.300 ± 0.135, P = 0.028), 60% (0.249 ± 0.109, P = 0.026), and 70% of MVC (0.245 ± 0.114, P < 0.001). A significant difference in EEG-β-PSD was also observed between 20% (0.313 ± 0.149) and 70% of MVC (P = 0.036). By contrast, no significant changes in EEG-β-PSD were observed in the SOL (all, P > 0.05).

Regarding EEG-γ-PSD, the main effects of the muscles (F_{1,10} = 24.927, P = 0.001) and contraction levels (F_{6,60} = 12.225, P < 0.001) were highly significant. As there was a significant interaction between muscle and contraction level on EEG-γ-PSD (F_{6,60} = 6.680, P < 0.001), the differences in EEG-γ-PSD between the muscles for each of the seven contraction levels and those among the contraction levels for each muscle were tested by post hoc comparisons. In the TA, EEG-γ-PSD at 70% of MVC (0.104 ± 0.028) was significantly greater than those at 10% (0.077 ± 0.026), 20% (0.077 ± 0.027), 30% (0.084 ± 0.026), 40% (0.085 ± 0.029) (all, P < 0.001), and 50% of MVC (0.089 ± 0.024, P = 0.004). The EEG-γ-PSDs at 50% (0.089 ± 0.024) and 60% of MVC (0.096 ± 0.030) were significantly greater than those at 10% (vs. 50%, P = 0.039; vs. 60%, P < 0.001) and 20% of MVC (vs. 50%, P = 0.046; vs. 60%, P < 0.001). No significant changes in EEG-γ-PSD were detected in the SOL (all, P > 0.05).

Figure 4 illustrates typical examples of EEG-EMG coherence spectra for all contraction levels for both the TA and SOL. The data shown are from three subjects who showed significant coherence at all contraction levels for both muscles. The TA showed a tendency for prominent coherence peaks to exist within the β-band during weak to moderate intensity of isometric voluntary contractions. Within the force range of 10–50% of MVC, the frequency at which the β-band peaks of coherence occurred was unchanged. Coherence peaks within the γ-band gradually increased, depending on the contraction levels, and two peaks of EEG-EMG coherence coexisted in both the β-band and γ-band at 40–50% of MVC. In such cases, there was a prominent dip of the coherence between the β-band peaks and γ-band peaks when the coherence spectra were observed in the frequency direction. Since not just one but several data points were continuously below the SL between the β-band and γ-band peaks of coherence, we judged that these two coherence peaks were the distinctive peaks. Under stronger contractions above 60% of MVC, significant EEG-EMG coherence only occurred in the γ-band, by replacing the β-band coherence. By contrast, for the SOL, the maximal peaks of EEG-EMG coherence were within the β-band across all contraction levels. Indeed, in subjects 1 and 3, the frequency at which the maximal peaks of coherence occurred did not change across all contraction levels. By contrast, in subject 10, the peak frequency of EEG-EMG coherence slightly increased with increasing contraction level, but it did not shift to the γ-band. None of the subjects showed clear frequency shifts in coherence from the β-band to the γ-band with increasing contraction level of the SOL.

Figure 5 shows the means ± SD for Cohβ-max (Fig. 5A) and Cohγ-max (Fig. 5B) at all contraction levels for both the TA and SOL. ANOVA revealed no significant difference in the Cohβ-max between the muscles (F_{1,10} = 0.957, P = 0.351), whereas the effects of the contraction levels on Cohβ-max were highly significant (F_{6,60} = 3.531, P = 0.005). Thus we conducted a post hoc analysis to examine the difference in Cohβ-max among the contraction levels for each muscle, separately. In the TA, the Cohβ-max at 10% of MVC (0.248 ± 0.158) was significantly greater than those at 50% (0.134 ± 0.084, P = 0.007), 60% (0.133 ± 0.062, P = 0.006), and 70% of MVC (0.094 ± 0.034, P < 0.001). A significant difference in Cohβ-max was also observed between 20% (0.185 ± 0.121) and 70% of MVC (P = 0.048). By contrast, Cohγ-max did not change significantly with changes in contraction level in the SOL (all, P > 0.05).
The main effects on Cohγ-max of the muscles (F_{1,10} = 11.323, P = 0.007) and contraction levels (F_{6,60} = 6.734, P < 0.001) were highly significant. As there was significant interaction between muscle and contraction level on Cohγ-max (F_{6,60} = 2.245, P = 0.049), the differences in Cohγ-max between the muscles for each of the seven contraction levels and those among the contraction levels for each muscle were tested by post hoc comparisons. For the TA, Cohγ-max was significantly greater at 70% of MVC (0.183 ± 0.087) than at 10% (0.094 ± 0.044, P = 0.004) and 20% of MVC (0.102 ± 0.039, P = 0.008). Cohγ-max at 60% of MVC (0.189 ± 0.106) was also significantly greater than those at 10% (P = 0.003) and 20% (P = 0.001) of MVC. For the SOL, Cohγ-max did not change significantly with changes in contraction level (all,
synchronized neural activities are unchanged within the lower cortex and the frequency band of the EMG coherence was only observed within the γ-band when the contraction level was above 60% of MVC. Thus the frequency shifts of EEG-EMG coherence from the β-band to γ-band in the TA seem to be related to contraction levels.

The present study detected a significant increase in the cortical γ-rhythm by increasing contraction level of the TA. Regarding the functional role of the cortical γ-rhythm, two possible mechanisms have been suggested: namely, a nonspecific cortical activation associated with attention to a very strong contraction, and a specific mode of functional coupling between the cortex and the contracting muscle (5). Mima et al. (33) demonstrated that the increased γ-band oscillation was not restricted to the area over the sensorimotor cortex, but was widely distributed over the frontocentral area, suggesting that the generator mechanism of the cortical γ-rhythm involves the large frontal cortical network, and that increased γ-band oscillation in EEG includes a general attention effect. However, they also reported that the distribution of significant cortico-muscular coherence was localized within the sensorimotor area during strong contraction (33). Thus, although both cognitive and motor control components are involved in the cortical γ-rhythm, the emergence of γ-band EEG-EMG coherence would imply a functional role played by the γ-band oscillatory drive from the cortex in motor control.

When performing strong contractions of the TA, the maximal firing rate of activated motor units reaches up to ~65 Hz, and new motor units are recruited at the same time, up to ~90% of MVC in the TA (7, 21, 53). It has been suggested that the high-frequency descending drive to the spinal motoneuron pool can be very powerful, leading to the entrainment of nearly all the motor units in a muscle (32). Thus, overall, it is suggested that the powerful γ-band oscillatory drive from the sensorimotor cortex contributes to both the elevation of discharge frequency of activated motor units and the recruitment of most of the motor units and, by grouping the activated motor units, generates the EMG Piper rhythm to achieve stronger muscle force.

**No Changes in the Frequency Band of EEG-EMG Coherence, Irrespective of the Contraction Levels in the SOL**

In contrast to the TA, the EEG signals did not include γ-band oscillations, even when performing strong contractions of the SOL, meaning that the peaks of EEG-EMG coherence stayed within the β-band, irrespective of the contraction levels. It is possible that both technical problems and physiological mechanisms account for the obtained results.

**Potential technical problems regarding EEG signal processing.** It could be claimed that the lack of cortical γ-rhythm observed in the SOL contractions may be caused by attenuation of the high-frequency component of the EEG signals by the skull and scalp (15, 33). In the case of the strong contractions of the TA, however, clear γ-band oscillations were observed in the EEG signals in the subjects who showed significant EEG-EMG coherence. Since the cortical neuron populations innervating in the SOL and TA activations are adjacent located deep in the cerebral sulcus, the low-pass filter characteristics of

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**DISCUSSION**

The present findings have suggested that the corticomuscular coupling shifts its frequency band from the β-band to γ-band with increasing the contraction levels in the TA, while the coupling stays within the β-band, irrespective of the contraction levels in the SOL. These findings would support our hypothesis that contraction level-related modulation patterns of the frequency characteristics of corticomuscular coupling differ between muscles with different muscle compositions and functions.

**Frequency Shifts in EEG-EMG Coherence From the β-Band to the γ-Band With Increasing Contraction Levels in the TA**

The frequency changes in EEG-EMG coherence, depending on the contraction level observed in the TA, were similar to the findings of Brown et al. (5), who also compared the frequency characteristics of EEG-EMG coherence between several contraction levels in the TA. For weak intensity (10–30%) of isometric voluntary contraction of the TA, the peaks of EEG-EMG coherence were observed within the β-band. Furthermore, the magnitude of the coherence did not change within this weak force range. These data suggest that the strength of the corticomuscular coupling and the frequency band of the synchronized neural activities are unchanged within the lower force range. Moderate (40–50%) contractions of the TA were characterized by two distinct coherence peaks, such as one in the β-band and another in the γ-band, while significant EEG-EMG coherence was only observed within the γ-band when the contraction level was above 60% of MVC. Thus the frequency shifts of EEG-EMG coherence from the β-band to γ-band in the TA seem to be related to contraction levels.

![Cohβ-max (A) and Cohγ-max (B) at all contraction levels for the TA and SOL. The data are shown as means ± SDs (solid circles: TA; shaded circles: SOL). The estimated SL is shown as a horizontal dashed line. *P < 0.05, **P < 0.01, ***P < 0.001, significant differences between the contraction levels within the same muscle. #P < 0.05, ##P < 0.01, significant differences between the muscles at the same contraction level.](image-url)
the skull and scalp would have limited impact on the EEG signals recorded in the present study.

Furthermore, when tasks, including synergistic activities of several muscles, are employed for humans, damping and phase collapse of the EEG signals might occur, owing to cross talk of the cortical signals to some contracting muscles. However, in the present study, we employed a body posture with the knee flexed at 90° to measure the EEG-EMG coherence for the SOL. When the knee is flexed deeper than 80°, the fascicle of the gastrocnemius, a biarticular plantar flexor synergist, becomes slack (52, 54), while the SOL, a single-joint plantar flexor, does not change its fascicle length (24). In such positions, the MVC force is known to be significantly decreased compared with that performed in the knee-extended position, because the gastrocnemius EMG activity is markedly depressed, owing to the muscle slackening (9). On the other hand, the EMG amplitudes of the SOL at the same relative contraction levels are almost equal between the knee-extended and knee-flexed positions (9). Since the body posture used in this study prominently reduced the contribution of the gastrocnemius muscle activity, the present study would be able to minimize the difficulty regarding the interpretation of the obtained EEG data. We believe that the body posture used in this study was appropriate to focus on the modulations of EEG-EMG coherence with changing contraction levels for the SOL.

In the present study, EEG was recorded with only five electrodes. Thus it is possible that the electrodes could not correctly record the activity of the relevant cortical neurons, because the cortical areas activated during contraction may change and/or expand at higher contraction levels, as previously reported using functional MRI (36, 55) or PET (11). However, unlike those studies, our subjects performed lower limb muscle contractions. As the foot representation area is distributed deep in the cerebral sulcus in a vertical direction, the somatotopic changes induced by changes in activation level are expected to be limited to the spatial sensitivity distribution of EEG (3–5 cm) (28). Changes in the activated motor area occurring in a vertical direction may influence EEG power, but coherence is known to depend on the amplitude ratio and phase difference between two signals, rather than the absolute value of the amplitudes (47). Therefore, although we cannot exclude the possibility that changes and/or expansion of the activated cortical area occurred in response to the increase in contraction level, this is unlikely to have a major impact on the present EEG-EMG coherence results.

It is also possible that the present EEG recordings were influenced by changes in the direction of activated cortical neurons in the motor area following changes in contraction level. It is known that EEG can detect radially and tangentially oriented sources, while MEG only detects sources oriented tangentially to the head (29, 37, 38, 59). Therefore, it seems unlikely that the orientation of the activated neurons would considerably affect the EEG recordings or EEG-EMG coherence measurements. Based on this assumption, we believe that the physiological mechanisms underlying the difference in contraction level-related modulation of EEG-EMG coherence between the TA and SOL are worthy of discussion. However, since γ-band oscillation in the EEG signals is weaker in its power than the dominant frequency component, it might be sensitive to the distribution of the electric field, depending on the direction of the current dipole. Therefore, we cannot fully exclude the possibility that the configuration of the EEG electrodes was differentially sensitive to the cortical areas innervating the SOL and TA muscles, thus influencing the present EEG and EEG-EMG coherence findings; i.e., the cortical γ-rhythm was observed under higher intensity contractions of the TA, but not under those of the SOL, resulting in the difference in modulation patterns of EEG-EMG coherence between the TA and SOL, with changes in contraction level.

Potential physiological mechanisms. There are several potential central mechanisms that can modulate the synchrony of the cortical cell populations in the sensorimotor cortex, thus causing the differences in EEG PSD and EEG-EMG coherence between the TA and SOL. It is possible that the local network properties within the sensorimotor cortex differ between these muscles. Indeed, by using a paired-transcranial magnetic stimulation paradigm, Chen et al. (6) demonstrated that the amounts of intracortical inhibition and facilitation differ among different representations of the human motor cortex. Unfortunately, to our knowledge, there have been no studies reporting differences in the intracortical mechanisms for inhibition and facilitation between the TA and SOL. However, if they exist, such mechanisms may account for the observed difference in the rhythmicity of the oscillatory EEG activity during strong contraction between the TA and SOL. Furthermore, the nonprimary motor cortex and/or basal ganglia may be candidates for a limiter of neural activity in the corticospinal tract. The nonprimary motor cortex is a well-known upstream module that regulates the synchronized activity of the cortical cell populations in the primary motor cortex. Indeed, Mima et al. (33) demonstrated that, when the EEG signal over the sensorimotor cortex shows γ-band activity during strong contraction, increased γ-band oscillations are also observed over the bilateral frontal areas, suggesting that the frontal cortical network plays a key role in modulating the synchrony of networks in the primary sensorimotor cortex. Moreover, a previous study demonstrated the presence of significant coherence between the local field potential of the subthalamic nucleus and EEG recorded over the supplementary motor cortex or over the sensorimotor cortex in both the β-band and γ-band during isometric wrist contraction (30). These data suggest that there may be some relative frequency selectivity in the communication between different motor structures. Thus it is possible that a basal ganglia-cortex loop may contribute to the regulation of synchronized activity of the cortical cell populations in the sensorimotor cortex. Thus, when performing strong contractions of the SOL, these central mechanisms might limit the increase in frequency of the synchronized oscillatory activities in the cortical cell populations innervating the SOL.

Furthermore, it is assumed that mechanisms that modulate motoneuron output synchrony exist at the spinal level, leading to the observed lack of changes in the frequency band of EEG-EMG coherence, irrespective of the contraction levels in the SOL. One of the possible neural circuits contributing to the reduction in frequency of oscillatory grouped firing of spinal motoneurons is recurrent inhibition via Renshaw cells (41). Renshaw cells receive excitatory input from motoneurons and feedback inhibition to the same motoneuron pool. In addition, as previously suggested (56), it is possible that spinal interneurons, which are supplied with a rich range of sensory inputs from the periphery, contribute to the damping of the oscillation of spinal motoneurons’ output. Such spinal factors also support
the limited frequency elevation of grouped firing of the SOL spinal motoneuron populations, leading to the absence of changes in the frequency band of corticomuscular coupling, irrespective of contraction level.

It is also known that there are some differences in the anatomical/physiological characteristics between the SOL and TA. Although type I fibers are dominant in both muscles in humans, the proportion of type II muscle fibers is ~15% higher in the TA than in the SOL (TA, 73.4% at surface and 72.7% at depth; SOL, 86.4% at surface and 89.0% at depth) (23). In addition, the muscle contractile properties differ between these muscles, i.e., the contraction time and half-relaxation time, estimated from the time course of single twitches elicited by supramaximal electrical nerve stimulation, are slower in the SOL (contraction time, 116.0 ± 9.0 ms; half-relaxation time, 98.5 ± 23.1 ms) (4) than in the TA (contraction time, 80.8 ± 13.0 ms; half-relaxation time, 93.6 ± 25.1 ms) (3). Furthermore, it was reported that the SOL is more resistant to muscle fatigue than the TA (3). In accordance with such differences in the anatomical/physiological characteristics, muscle-dependent activation strategies to alter the contraction levels might be mounted in the central nervous system.

**Functional Significance of the Present Findings**

Next, we consider the potential physiological meaning of the present findings regarding the absence of frequency changes of EEG-EMG coherence observed in the SOL, irrespective of the contraction levels, and the frequency shift in EEG-EMG coherence from the β-band to the γ-band in the TA with increasing contraction level. Using the interpolated twitch technique, Behm et al. (2) reported that the extent of muscle inactivation or inability to produce maximum force is greater in the SOL than in the TA. This means that maximizing the force generation capacity voluntarily is more difficult in the SOL than in the TA. Although both the SOL and TA rely on recruitment and firing rate modulation of their motor units over the full range of contraction strength, the firing frequency during high force production is much lower in the SOL (5–25 Hz) (4, 39) than in the TA (25–65 Hz) (7, 21, 53). The firing rate itself does not individually or directly contribute to EMG power, but an increase in motor unit firing rate in the TA during high-intensity contractions would be considerably needed to achieve γ-band synchrony of the motoneuron pool. This is because it is difficult to assume that γ-band synchrony in motoneuron populations is achieved with a low (α-band or β-band) firing rate of individual neurons. Therefore, the motor unit firing property reported previously (i.e., the increase in motor unit firing rate caused by increases in contraction level in the TA, but not in the SOL) may be associated with the frequency shift of EEG-EMG coherence at high contraction levels, which was first observed in this study. We suggest that, in the SOL, the absence of frequency increases of corticomuscular coupling makes it difficult to fully exert the force generation capacity voluntarily.

The above-mentioned mechanism would be attributed to the functional role of the SOL in the activities of daily living. The SOL is an anti-gravitational muscle and must be activated in a sustained manner to maintain body posture without fatigue. Indeed, the SOL shows more tonic muscle activation patterns than the TA during standing (31, 45) and walking (13, 17, 35). Furthermore, as a result of long-term (7-h) EMG recording of the lower leg muscles during normal daily routines, it was reported that the summed duration of EMG bursts in the activities of daily living is significantly longer in the SOL than in the TA (46). Thus it is assumed that the central nervous system needs to include an implemental strategy to reduce muscle fatigue in the SOL. We suggest the possibility that the absence of frequency changes of EEG-EMG coherence, irrespective of the contraction levels in the SOL, would reflect such a neural activation strategy. In other words, by maintaining the rhythmicity of corticomuscular coupling within the β-band, irrespective of the contraction levels, the central nervous system would limit the increment in the frequency of rhythmic grouped discharges in the spinal motoneuron populations, thereby making it possible to delay the development of muscle fatigue.

**Conclusions**

The present data have suggested a difference in the modulation patterns of corticomuscular coherence with changing contraction levels between the TA and SOL. Indeed, the TA shifted the EEG-EMG coherence from the β-band to the γ-band with increasing contraction level, whereas the maximal peak of EEG-EMG coherence in the SOL stayed within the β-band, irrespective of the contraction levels. These findings suggest that the central nervous system regulates the frequency of corticomuscular coupling to exert the desired levels of muscle force and, notably, that the applicable rhythmicity of the coupling to perform strong contractions differs between muscles, depending on the physiological muscle compositions and functions.

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**DISCLOSURES**

No conflicts of interest, financial or otherwise, are declared by the author(s).

**AUTHOR CONTRIBUTIONS**

J. Ushiyama and J. Ushiba developed conception and design of research; J. Ushiyama performed experiments; J. Ushiyama analyzed data; J. Ushiyama, Y.M., T.F., T.T., K.H., A.K., M.L., and J. Ushiba approved final version of manuscript; J. Ushiyama and J. Ushiba edited and revised manuscript.

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