Between-subject variance in the magnitude of corticomuscular coherence during tonic isometric contraction of the tibialis anterior muscle in healthy young adults

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Submitted 7 March 2011; accepted in final form 4 June 2011

Ushiyama J, Suzuki T, Masakado Y, Hase K, Kimura A, Liu M, Ushiba J. Between-subject variance in the magnitude of corticomuscular coherence during tonic isometric contraction of the tibialis anterior muscle in healthy young adults. J Neurophysiol 106: 1379–1388, 2011. First published June 8, 2011; doi:10.1152/jn.00193.2011.—Oscillatory activity of the sensorimotor cortex has been reported to show coherence with muscle activity in the 15- to 35-Hz frequency band (β-band) during weak to moderate intensity of isometric contraction. The present study examined the variance of the magnitude of the corticomuscular coherence across a large number of subjects. We quantified the coherence between EEG over the sensorimotor cortex and rectified electromyogram (EMG) from the tibialis anterior muscle during tonic isometric contraction at 30% of maximal effort in 100 healthy young individuals. We estimated the maximal peak of EEG-EMG coherence (Cohmax) and the ratio of the sum of the autopower spectral density function within the β-band to that of all frequency ranges for both EEG (EEGβ-PSD) and EMG (EMGβ-PSD) signals. The frequency histogram of Cohmax across all subjects showed a broad bell-shaped continuous distribution (range, 0.048–0.816). When the coherence was thresholded at the estimated significance level of P < 0.05 (0.114), 46 out of 100 subjects showed significant EEG-EMG coherence. Cohmax occurred within the β-band in the majority of subjects who showed significant EEG-EMG coherence (n = 43). Furthermore, Cohmax showed significant positive correlations with both EEGβ-PSD (r = 0.575, P < 0.001) and EMGβ-PSD (r = 0.606, P < 0.001). These data suggest that even during simple tonic isometric contraction, the strength of oscillatory coupling between the sensorimotor cortex and spinal motoneurons varies among individuals and is a contributory factor determining muscle activation patterns such as the degree of grouped discharge in muscle activity within the β-band for each subject.

electroencephalogram; electromyogram; EEG-EMG coherence; β-band oscillation

IT IS WELL-ESTABLISHED THAT oscillatory neural activity of the sensorimotor cortex shows coherence with electromyographic activity in contralateral limb muscles within the 15- to 35-Hz frequency band (β-band) during weak-to-moderate intensity tonic isometric contraction in both animals (Baker et al. 1997; Witham et al. 2010) and humans (Conway et al. 1995; Farmer et al. 1993; Gross et al. 2000; Halliday et al. 1998; Kilner et al. 2000; Kristeva et al. 2007; Mima et al. 2000; Salenius et al. 1997; Witte et al. 2007). As several previous studies examining a phase delay between the synchronized EEG or magnetoencephalogram (MEG) activity over the sensorimotor cortex and electromyogram (EMG) activity of contracting muscle demonstrated that the two signals are phase locked and that EEG/MEG precedes EMG (Baker et al. 1997; Brown et al. 1998; Conway et al. 1995; Halliday et al. 1998; Mima et al. 2000), the corticomuscular coherence was initially assumed to be an efferent phenomenon. However, more recently, a contribution of sensory afferent feedback to the generation and/or modulation of corticomuscular coherence has been indicated based on studies reporting modulation of the magnitude of MEG-EMG coherence after induction of ischemic sensory deafferentation (Pohja and Salenius 2003) and that of phase between EEG and EMG following arm cooling (Riddle and Baker 2005). Furthermore, several recent studies have reported the modulation of the corticomuscular coherence following visuomotor skill learning (Perez et al. 2006), immobilization (Lundbye-Jensen and Nielsen 2008), and development (Grazia di et al. 2010; James et al. 2008), suggesting changes of sensori-motor integration processes between the cortex and peripheral motoneurons as part of the motor adaptation process.

It has been reported that there is between-subject variance in the magnitude of corticomuscular coherence. For example, stable and high EEG-EMG coherence spectra within the β-band were observed in five of eight subjects during tonic isometric contraction of the abductor pollicis brevis muscle at 10–20% of maximal voluntary contraction (MVC) (Mima et al. 2000). Furthermore, the peak value of EEG-EMG coherence within the β-band during tonic isometric contraction of the tibialis anterior muscle (TA) at 10–15% of MVC varied from 0.05 to 0.4 among 11 young healthy volunteers (Perez et al. 2006). We recently reported that the magnitude of EEG-EMG coherence varies among individuals and suggested that EMG signals in subjects with greater EEG-EMG coherence seem to show increased oscillatory activity within the β-band (Hashimoto et al. 2010; Ushiyama et al. 2011). Furthermore, we found that when muscle fatigue develops in the TA, the magnitude of EEG-EMG coherence is enhanced with increased force fluctuation (Ushiyama et al. 2011). Based on these findings, we suggest that the strength of corticomus-
MATERIALS AND METHODS

EEG and EMG recordings. Surface EMG recordings were made from the TA, over the muscle belly, using bipolar Ag/AgCl electrodes with a diameter of 10 mm and an interelectrode distance of 20 mm. EEG recordings were made from the scalp near the sensoriomotor cortex using five Ag/AgCl surface electrodes with a diameter of 5 mm, placed at Cz (defined by the international 10–20 system) and 20-mm frontal, 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 (Hjorth 1975). Impedance of the EEG and EMG electrodes was kept below 5 and 20 kΩ, respectively, during the recording.

All analog EEG and EMG signals were amplified and band-pass filtered (EEG, 0.5–100 Hz; EMG, 1–500 Hz) using a standard EEG or EMG recording system (Neuropack ME-2200 or Neuropack ME-4308; Nihon Kohden, Tokyo, Japan). Force signal was recorded with a force transducer (TU-BR; TEAC, Tokyo, Japan) attached to the footplate. All 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 protocol. Each subject was comfortably seated on a chair. Before experimentation, subjects performed an isometric dorsiflexion with maximal effort lasting ~3 s. MVC force was determined as a peak value of dorsiflexion force over the period of stable force output. After a sufficient rest period of 90–120 s, subjects performed tonic isometric contraction of the TA at 30% of MVC for 60 s. As is the case with our recent studies (Hashimoto et al. 2010; Ushiyama et al. 2010, 2011), we used 30% of MVC as the contraction level for measuring the EEG-EMG coherence because of the following reasons: 1) the magnitude of β-band corticomuscular coherence is not affected by the contraction levels in weak to moderate intensity of isometric contraction (Brown et al. 1998; Mima et al. 1999); 2) compared with lower contraction levels, we can observe the β-band oscillations in EMG signals more clearly; and 3) we can avoid the effects of muscle fatigue on EEG-EMG coherence because it takes much longer than 60 s to induce muscle fatigue for the TA by sustained isometric dorsiflexion at 30% of MVC (Beck et al. 2005; Griffith et al. 2010). During the task, the dorsiflexion force was visually fed back on the computer screen positioned 1.2 m in front of the subjects, and the subjects were instructed to maintain their exerted force as close as possible to the line corresponding to 30% of their MVC force. To confirm the reproducibility of the magnitude of EEG-EMG coherence during tonic isometric contraction, 40 out of 100 subjects were randomly selected and performed the same task 3 times during the same experimental sessions with the same EEG and EMG electrode positions.

Data analysis. Before frequency analyses, we assessed the stationarity of obtained time-series EEG and EMG signals by revising the existence of unit roots of the associated characteristic equation of the autoregressive process using the augmented Dickey-Fuller test (Luo et al. 2010). As unit roots were not present in all of the raw EEG and EMG data, the obtained data were considered as weak stationary at the very least.

EMG signals were rectified, as full wave rectification is known to provide the temporal pattern of grouped firing motor units (Halliday and Farmer 2010; Halliday et al. 1995). Raw EEG and rectified EMG signals were segmented into artifact-free epochs of 1,024-ms duration, with no overlap (58 epochs). Each 1,024-ms data segment was Hann-windowed to reduce spectral leakage (Baker et al. 1997; Farmer et al. 1993; Gross et al. 2000). Correlations between EEG and rectified EMG \(C_{\text{EEG}}(f)\) were calculated by coherence using the following equation (Halliday et al. 1995):

\[
\text{coherence} = \frac{|C_{\text{EEG}}(f)|^2}{C_{\text{EEG}}^2(f) \cdot C_{\text{EMG}}^2(f)}
\]
To examine the relationships between the strength of EEG-EMG coherence and the magnitude of \( \beta \)-band oscillations in EEG and EMG signals, we also determined the ratio of the sum of the auto-PSD functions of the EEG and the rectified EMG signals throughout the segments. Coherence function provides a normative value of the EEG-EMG coherence (Cohmax), the maximal peaks of the coherence spectrum (Cohmax) and the maximal voluntary contraction (MVC). We calculated \( f \) the maximal value of the EEG-EMG coherence (Cohmax), 2) the frequency where Cohmax was observed (FP), 3) the frequency where the coherence spectrum 1st met the estimated significance level (SL) when traced backward from FP (F1), and 4) the frequency where the coherence spectrum 1st met the SL when traced forward from FP (F2).

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

where \( P_{xx}(f) \) and \( P_{yy}(f) \) are the averaged autopower spectral density (PSD) functions of the EEG and the rectified EMG signals throughout the segments for a given frequency \( f \), respectively, and \( P_{xy}(f) \) is the averaged cross-PSD function between EEG and rectified EMG signals throughout the segments. Coherence function provides a normative measure of linear correlation on a scale of 0 – 1, where 1 indicates a perfect linear correlation. We also estimated the phase spectrum, as previously reported (Baker et al. 1997; Conway et al. 1995; Farmer et al. 1993; Gross et al. 2000; Halliday et al. 1998; Kilner et al. 2000; Kristeva et al. 2007; Mima et al. 2000; Salenius et al. 1997; Witham et al. 2010; Witte et al. 2007), whereas only 3 subjects showed a Cohmax > 40 Hz, as previ-
Surprisingly, we found five subjects with a Cohmax value >0.5. Such a high magnitude of EEG-EMG coherence has not been previously reported. It is possible that such strong correlations between Cohmax and EEGβ-PSD and between Cohmax and EMGβ-PSD resulted from inclusion of several subjects with very high levels of β-band EEG-EMG coherence. Thus, we also calculated the Pearson correlation coefficients between Cohmax and EEGβ-PSD and between Cohmax and EMGβ-PSD for subjects with Cohmax values <0.5 (n = 95), according to the previously reported range of the subjective variability of β-band EEG-EMG coherence in the TA of healthy individuals (Gross et al. 2000; Perez et al. 2006). In this data set, we still detected significant positive correlations between Cohmax and EEGβ-PSD (r = 0.373, P < 0.001) and between Cohmax and EMGβ-PSD (r = 0.423, P < 0.001).

The histogram of the obtained EMGβ-PSD values from all subjects is shown in Fig. 4A. Based on the histogram, we divided the subjects into two groups of EMGβ-PSD values greater (GD+, n = 44) or smaller (GD−, n = 56) than the mean EMGβ-PSD (0.209) to examine differences in the strength of the EEG-EMG coherence depending on the magnitude of β-band oscillation in the EMG. Group data (means ± SD) for Cohmax in GD+ and GD− are shown in Fig. 4B. Cohmax values were significantly greater in GD+ (0.216 ± 0.184) than in GD− (0.122 ± 0.068; z = 2.125, P = 0.034).

On the basis of the results in Fig. 3, A and B, we investigated between-subject variance in β-band oscillation in EEG and EMG signals related to the magnitude of EEG-EMG coherence by carefully reviewing raw signals and PSDs of EEG and EMG. Examples of raw EEG and EMG signals, power spectra for the EEG and rectified EMG signals, and coherence and phase spectra between the EEG and rectified EMG signals are shown in Fig. 5. Data from subjects who showed greater Cohmax value are shown in Fig. 5A (Cohmax = 0.816) and

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**Fig. 3.** Correlation between the magnitude of EEG-EMG coherence and the degree of β-band oscillation in EEG or EMG signal. A: relationship between Cohmax and EEGβ-power spectral density (PSD). B: relationship between Cohmax and EMGβ-PSD. Linear regression equations and Pearson correlation coefficients (r) are represented in both figures. Black line indicates the estimated regression line. Gray lines indicate ±2 SD from the regression line. The SL is shown as vertical dashed lines.

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**Fig. 4.** Difference in the magnitude of EEG-EMG coherence between subjects with β-band grouped discharge in EMG and those without grouped discharge. A: histogram of the magnitude of EMGβ-PSD from all subjects. A total of 100 EMGβ-PSD values are plotted. We divided subjects into 2 groups defined by EMGβ-PSD values greater (GD+: n = 44) or smaller (GD−: n = 56) than the mean value (0.209). B: group data (means ± SD) for Cohmax in GD+ and GD−. Significant differences between GD+ and GD− are shown (*P < 0.05).
Fig. 5. Examples of raw EEG signals, raw EMG signals, PSDs for the EEG and rectified EMG signals, and coherence and phase spectra between EEG and rectified EMG signals during tonic isometric contraction. A and B: data for subjects with a greater Cohmax value across all subjects (A, Cohmax = 0.816; B, Cohmax = 0.658). C and D: data for subjects with moderate EEG-EMG coherence (C, Cohmax = 0.331; D, Cohmax = 0.414). E–H: data for subjects with an EEG-EMG coherence not significant across the entire frequency range (E, Cohmax = 0.048; F, Cohmax = 0.078; G, Cohmax = 0.106; H, Cohmax = 0.094). In the coherence spectra, the SL is shown as horizontal dashed lines.
Fig. 5B (Cohmax = 0.658). EEG and EMG signals oscillated synchronously within the β-band. Indeed, both EEG and EMG PSDs show distinct peaks in the β-band where the Cohmax was observed. Furthermore, in the frequency range where the coherence spectrum exceeded the SL, the phase spectrum showed a positive slope, indicating that EEG precedes EMG. Data from subjects who showed moderate EEG-EMG coherence are shown in Fig. 5C (Cohmax = 0.331) and Fig. 5D (Cohmax = 0.414). There were weaker but still obvious oscillatory activities in EEG and EMG signals in the β-band, resulting in significant but less evident EEG-EMG coherence in the β-band compared with Fig. 5, A and B. Data from subjects whose EEG-EMG coherence curve did not exceed the SL across the entire frequency range are shown in Fig. 5, E–H (E, Cohmax = 0.048; F, Cohmax = 0.078; G, Cohmax = 0.106; H, Cohmax = 0.094). The subjects with no significant EEG-EMG coherence often showed less rhythmic or synchronous oscillations in EEG and EMG signals, as observed in Fig. 5, E and F. However, as observed in Fig. 5G, there were some subjects whose EMG signal showed clear grouped discharge within the β-band, although the EEG signal did not fluctuate rhythmically and EEG-EMG coherence was not significant. These subjects exceeded +2 SD from the regression line with respect to the correlation between Cohmax and EMGβ-PSD as shown in Fig. 3B. By contrast, other subjects exhibited clear β-band oscillation in the EEG signal, although the EMG signal did not show clear grouped discharge and EEG-EMG coherence was not significant (Fig. 5H). These subjects exceeded +2 SD from the regression line with respect to the correlation between Cohmax and EEGβ-PSD as shown in Fig. 3A.

**DISCUSSION**

In the present study, we examined EEG-EMG coherence during tonic isometric contraction of the TA across 100 healthy young subjects and represented the distribution of the magnitude of EEG-EMG coherence. As some previous studies reported with a small number of subjects (Mima et al. 2000; Perez et al. 2006), the present study demonstrated a between-subject variance in the magnitude of EEG-EMG coherence, i.e., the histogram of Cohmax across all subjects showed a broad bell-shaped continuous distribution (range, 0.048–0.816), and 46 out of 100 subjects showed significant EEG-EMG coherence. Cohmax occurred within the β-band in the majority of subjects who showed significant EEG-EMG coherence (n = 43). Furthermore, Cohmax values showed significant positive correlations with both EEGβ-PSD and EMGβ-PSD. These data suggest that even during simple tonic isometric contraction, the strength of oscillatory coupling between the sensorimotor cortex and spinal motoneurons varies among individuals and is a contributory factor determining muscle activation patterns such as the degree of grouped discharge in muscle activity within the β-band for each subject.

**Potential mechanisms of between-subject variance in the magnitude of corticomuscular coherence.** Previous monkey studies demonstrated the occurrence of β-band oscillations in local field potentials and unit activity in the primary motor cortex when performing motor tasks (Donoghue et al. 1998; Murthy and Fetz 1992, 1996a,b; Sanes and Donoghue 1993). On the basis of these findings, coherence between EEG/MEG and EMG has been evaluated to investigate how the synaptic drive from the sensorimotor cortex generates and/or modulates spinal motoneuron activity during voluntary contraction in humans. Corticomuscular coherence was initially assumed to be mediated by fast corticospinal axons and their monosynaptic connections to spinal motor neurons (Conway et al. 1995). This assumption indicates that oscillatory coupling between cortical activity recorded by EEG and muscle activity recorded by EMG in the β-band may reflect discharge of corticospinal cells in this frequency range (Farmer et al. 1993). In addition, several studies have demonstrated a phase delay between the synchronized cortical and EMG oscillations, indicating that the two signals are phase locked and that cortical activity precedes EMG (Baker et al. 1997; Brown et al. 1998; Conway et al. 1995; Halliday et al. 1998; Mima and Hallett 1999). Based on these findings, it was suggested that EMG oscillations largely resulted from the sensorimotor motor cortex neural activity transmitted to the spinal motoneurons via corticospinal pathways.

The simplest interpretation of the observed between-subject variance in EEG-EMG coherence during tonic isometric contraction is that the tendency of the population of cortical neurons to discharge in synchrony differs among individuals (Lundby-Jensen and Nielsen 2008), i.e., a greater EEG-EMG coherence implies a higher level of synchronization of the activated cortical neurons that generate grouped discharge in EMG within the β-band, whereas a smaller EEG-EMG coherence reflects that the discharge frequency of the cortical neurons is more variable and not synchronized. This assumption is supported by the present findings that the magnitude of EEG-EMG coherence showed a significant positive correlation to the magnitude of β-band oscillation in EEG and EMG signals, as represented in Fig. 3. Thus it is likely that the tendency of the cortical cell population to discharge in synchrony modulates the degree of grouped discharge in EMG within the β-band and therefore may also account for the observed variation in the magnitude of EEG-EMG coherence among individuals.

Several recent studies have suggested that the mechanism of corticomuscular coherence may be more complex. Indeed, it was demonstrated that administration of benzodiazepine markedly enhanced the power of the oscillatory EEG signal but left the magnitude of EEG-EMG coherence unchanged, indicating that corticomuscular coherence cannot be explained by simple propagation of oscillations from the cortex to the muscle via descending pathways (Baker and Baker 2003). Furthermore, several recent studies have demonstrated that the somatosensory system is important in generating and/or modulating corticomuscular coherence. For example, the magnitude of MEG-EMG coherence decreased after ischemia-induced sensory deafferentation (Pohja and Salenius 2003), whereas changes in the phase between EEG and EMG signals 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 (Riddle and Baker 2005). Furthermore, Ia afferent spiking in monkeys showed coherence with oscillatory EMG activity over a wide frequency range including the β-band, providing direct evidence for ascending transmission of oscillatory information (Baker et al. 2006). As the densities of the somatosensory receptors likely vary among individuals, the extent to which the sensorimotor cortex receives inputs from the receptors may
contribute to determine the magnitude of corticomuscular coherence of each subject.

It is also assumed that mechanisms reducing oscillations of the motoneuron output exist at the spinal level, although oscillatory inputs from the sensorimotor cortex actually transmit via corticospinal pathways. Indeed, as observed in Fig. 3A, there were subjects who actually showed clear β-band oscillation in EEG signal but did not show significant EEG-EMG coherence. In these subjects, β-band oscillations were not observed in EMG signals as represented in Fig. 5H. One of the possible neural circuits contributing to reduce oscillations in motoneuron firing is recurrent inhibition via Renshaw cells. Renshaw cells are known to receive excitatory input from motoneurons and feedback inhibition to the same motoneuron pool (Renshaw 1941). A recent computational modeling study demonstrated a reduction of corticospinal coherence by Renshaw cell inhibitory feedback (Williams and Baker 2009). Furthermore, as previously suggested (Williams et al. 2010), it is also possible that spinal interneurons, which are supplied with a rich range of sensory inputs from the periphery, contribute to the damping of β-band oscillation of spinal motoneuron firing. Overall, these data suggest that the extent of reducing oscillation at the spinal level modulates the degree of grouped discharge in EMG within the β-band and therefore influences the magnitude of EEG-EMG for each subject.

It is possible that between-subject variance in the magnitude of EEG-EMG coherence only reflects whether the EEG electrodes successfully recorded the activity of the relevant cortical neurons, which is dependent on several biological factors including the orientation of the corticospinal neurons relative to the electrodes, the depth of the corticospinal neurons relative to the scalp, and the thickness of the skull and skull. Indeed, the electrical field measured by EEG is known to depend on these factors (Malmivuo et al. 1997; Nunez 1989; Olejniczak 2006; Yan et al. 1991). Notably, the orientation of activated neurons may affect the characteristics of the EEG signal obtained. Recent monkey studies demonstrated that the oscillations are also present in the primary somatosensory cortex and that there is β-band coherence between the primary somatosensory cortex and primary motor cortex (Murthy and Fetz 1992; Witham et al. 2007, 2010). If the activated neurons in the primary somatosensory cortex and those in the primary motor cortex are directly opposed, both signals could cancel each other, and, as such, EEG electrodes would be unable to successfully detect motor-related cortical neuron activity. Indeed, as shown in Fig. 3B, there was variance in EEG-β-PSD values even within the subjects whose Cohmax values were below the SL. As for the subjects who showed larger EMG/β-PSD but did not show significant EEG-EMG coherence, as represented in Fig. 5G, prominent β-band oscillations were not observed in the EEG signal. These findings suggest the possibility that in such subjects, although relevant cortical neurons actually activated rhythmically, the EEG electrodes did not record the activity correctly, resulting in a smaller magnitude of EEG-EMG coherence. However, when observing the entire trend for 100 subjects, Cohmax showed significant positive correlations with both EEGβ-PSD and EMGβ-PSD. If the magnitude of EEG-EMG coherence were determined only by whether motor-related cortical neuron activity was correctly detected from EEG electrodes, Cohmax would not show a positive correlation with EMGβ-PSD. Thus, although technical factors may determine whether significant β-band EEG-EMG coherence is detected, they have little impact on the subjective variability of β-band EEG-EMG coherence when it is present. We believe that physiological mechanisms behind the observed between-subject variance in the magnitude of EEG-EMG coherence are worthy of discussion and that there is a difference in the strength of oscillatory coupling between the sensorimotor cortex and spinal motoneurons when performing tonic isometric contraction among healthy adults.

Although the histogram of Cohmax showed a broad bell-shaped continuous distribution, it was asymmetric and considerably right-skewed. According to a previous study (Carter et al. 1973), if coherence is determined from a small number of data epochs, the estimated magnitude of coherence is actually largely biased from the true value. Furthermore, since the size of the error increases in cases with a smaller true magnitude of coherence, the distribution of coherence is actually right-skewed. However, by determining the coherence from a sufficient number of data epochs (~60 epochs), the bias of the coherence estimator can be considerably reduced, i.e., even when the true magnitude of coherence is <0.1, the possible error from the true magnitude of coherence is ~0.05 (Carter et al. 1973). Thus, although as for subjects with Cohmax values below the SL, the estimated coherence value may be slightly biased, but this error would only have a small physiological impact. Furthermore, for subjects where the true magnitude of coherence is >0.2, the possible error converges to a smaller value (<0.03). Overall these data indicate that the coherence estimator bias would have minimal impact on our results. Thus we suggest that the magnitude of corticomuscular coherence is actually distributed asymmetrically in healthy young adults and is not simply a manifestation of the right-skewed nature of coherence estimator.

Functional significance of between-subject variance in the magnitude of corticomuscular coherence. This is the first study to evaluate quantitatively the relationship between the magnitude of EEG-EMG coherence and β-band oscillations in the EMG signals. Indeed, muscle activation patterns during tonic isometric contraction obviously differed among subjects depending on the magnitude of EEG-EMG coherence, i.e., subjects with greater EEG-EMG coherence showed a more prominent group discharge in EMG signals within the β-band, resulting in a significant positive correlation between Cohmax and EMGβ-PSD. As such, rhythmic EMG bursts may indicate the presence of physiological leg tremor, and although we did not directly quantify the tremor by an accelerometer, the magnitude of corticomuscular coherence would be a determinant of the extent to which the exerted force fluctuates during tonic isometric contraction for each subject. In support of this assumption, we recently reported that muscle fatigue enhances the magnitude of EEG-EMG coherence, accompanied by increased force fluctuation during sustained isometric contraction (Ushiyama et al. 2011). Furthermore, the magnitude of EEG-EMG coherence is smaller in well-trained subjects, such as weightlifters, we suggested that reduced corticomuscular coupling reflects a motor adaptation in athletes for stabilizing force fluctuations during postural tasks (Ushiyama et al. 2010). Although several hypotheses have been proposed, the functional significance of the coupling has remained unclear in the literature (Baker and Baker 2003; Kilner et al. 1999; Riddle and Baker 2005; Salenius et al. 1997). Our data suggest a
potential effect of corticomuscular coherence on motor performance, where the strength of corticomuscular coupling is an important factor regulating the steadiness of motor output.

Although one concern might be that the discrete rhythmic EMG bursts observed in the subjects with much greater EEG-EMG coherence are pathological, neurological examination and neurophysiological investigations were normal in these subjects. Moreover, on direct questioning, this group of subjects denied any problems performing activities of daily living. Although the EMG signals during isometric contraction are known to show coherence with physiological tremor signals measured by accelerometer within the β-band (Halliday et al. 1999), the β-band component of physiological tremor is small in amplitude compared with the α-band component. Thus it is possible that because of the low amplitude of tremor, these subjects were not diagnosed with neurological disorders, whereas at the subclinical level, the degree of grouped discharge in EMG within the β-band is related to motor performance such as force steadiness. As described, the significant positive correlation between Cohmax and EMGβ-PSD suggests that the strength of corticomuscular coupling determines the magnitude of β-band oscillation in muscle activity, which may influence the amplitude of physiological leg tremor. Conversely, the tremor may also influence the magnitude of EEG-EMG coherence directly through somatosensory feedback systems or indirectly by introducing a visuomotor error (as subjects were required to stabilize their force output to the target force level as close as possible by using visual feedback system). Indeed, when the subjects were divided into two groups depending on the magnitude of β-band oscillations in the EMG signals, the subjects with rhythmic EMG bursts (GD+) showed significantly greater EEG-EMG coherence than those without rhythmic EMG bursts (GD−). Although further investigation is required to verify the association between the magnitude of EEG-EMG coherence and the amplitude of tremor by direct monitoring of tremor using an accelerometer, our data suggest a potential interaction between corticomuscular coherence and physiological tremor.

Surprisingly, there were 5 subjects with a Cohmax value >0.5 in the present study. Such a high magnitude of EEG-EMG coherence has not been previously reported. One possible explanation is that differences in the recorded muscle may lead to differences in the magnitude of EEG-EMG coherence. The majority of previous studies examining corticomuscular coherence in humans have used finger or hand muscles (Baker and Baker 2003; Conway et al. 1995; Farmer et al. 1993; Graziadio et al. 2010; James et al. 2008; Kilner et al. 1999, 2000; Kristeva et al. 2007; Lundbye-Jensen and Nielsen 2008; Mima et al. 2000; Pohja and Salenius 2003; Salenius et al. 1997). By contrast, we recorded EMG from the TA based on our previous finding that the distally located lower limb muscles, including the TA, show the greatest EEG-EMG coherence among various upper and lower limb muscles (Ushiyama et al. 2010). Indeed, other recent studies using the TA as the recorded muscle reported relatively large coherence values in some subjects (Gross et al. 2000; Hashimoto et al. 2010; Perez et al. 2006). In addition, the characteristics of the subjects would also influence the obtained magnitude of EEG-EMG coherence. As described, we recently reported training-related reduction of the magnitude of EEG-EMG coherence in ballet dancers and weightlifters (Ushiyama et al. 2010). If other previous studies mainly recruited subjects who were habituated to steady contraction (for example, members of the laboratory), although not to the extent of athletes, it would be possible that obtained EEG-EMG coherence converged to smaller values. As we selected 100 untrained, naïve healthy young volunteers as subjects in the present study, we would obtain a larger between-subject variance in the magnitude of EEG-EMG coherence.

Corticomuscular coupling has been suggested to play a role in sensorimotor integration processes within the motor system (Conway et al. 1995; Gross et al. 2000; Salenius et al. 1997). Indeed, several recent studies have reported the modulation of corticomuscular coherence following visuomotor skill learning (Perez et al. 2006), immobilization (Lundbye-Jensen and Nielsen 2008), and development (Graziadio et al. 2010; James et al. 2008), suggesting changes of sensorimotor integration processes between the cortex and peripheral neurons as part of the motor adaptation process. Taken together with the observed between-subject variance in the magnitude the EEG-EMG coherence, there is a possibility that sensorimotor integration processes in the motor system during motor adaptation differ among individuals depending on the innate strength of corticomuscular coupling. Future studies are required to determine differences in modulation processes of corticomuscular coherence and task performance by motor learning among individuals.

Conclusions. In the present study, we have demonstrated that the magnitude of EEG-EMG coherence during tonic isometric contraction of the TA exhibited a broad bell-shaped continuous distribution. When the coherence was thresholded at the SL (0.114, P < 0.05), 46 out of 100 subjects showed significant EEG-EMG coherence. Furthermore, the magnitude of EEG-EMG coherence showed significant positive correlations with the magnitude of β-band oscillations in both EEG and EMG signals. These data suggest that even during simple tonic isometric contraction, the strength of oscillatory coupling between the sensorimotor cortex and spinal motoneurons varies among individuals and is a contributory factor determining muscle activation patterns such as the degree of grouped discharge in muscle activity within the β-band for each subject.

GRANTS

The present study was supported by the Strategic Research Program for Brain Sciences (SRPBS) from the Ministry of Education, Culture, Sports, Science, and Technology (MEXT), Japan.

DISCLOSURES

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

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