Beta-range EEG-EMG coherence with isometric compensation for increasing modulated low-level forces

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Abstract

Corticomuscular synchronization has been shown to occur in beta- (15-30Hz) and gamma-range (30-45Hz) during isometric compensation of static and dynamic (periodically modulated) low-level forces, respectively. However, it is still unknown to what extent these synchronization processes in beta- and gamma-range are modified with increasing modulated force. We addressed this question by investigating the corticomuscular coherence (CMC) between the electroencephalogram (EEG) and electromyogram (EMG) from the first dorsal interosseus muscle (FDI), as well as the cortical and muscular spectral power during a visuomotor task, where different levels of a dynamic (modulated) force were used. Seven healthy right-handed female subjects compensated dynamic forces at 8, 16 and 24% of the maximal voluntary contraction (MVC) isometrically with their right index finger. Under the three conditions investigated, we found a broad-band CMC comprising both beta- and gamma-range and peaking at approx. 22 Hz within the beta band. This broad-band coherence increased linearly with higher force level. A separate analysis of the gamma-range CMC did not show significant modulation of the CMC by the force levels. EEG- and EMG spectral power did not show any significant difference among the three force conditions.

Our results favour the view that the function of beta-range CMC is not specific for low-level static forces only. The sensorimotor system may resort to stronger and also broader beta-range CMC to generate stable corticospinal interaction during increased force level, as well as when compensating for dynamic modulated forces. This finding re-enforces the importance of the beta-range EEG-EMG coherence in sensorimotor integration.
**Introduction**

Much attention has been given to the functional organization of the corticospinal system and the mechanisms of muscle control by the CNS and in particular to the universal mechanism of neuronal interaction via synchronization, which plays a relevant role in the effective coordination between the cortical motor areas and the muscles. This synchronization mechanism can be described by the coherence function for different frequency ranges. During maintained motor contraction the cortical motor areas and the muscles are synchronized in beta-range as shown in monkeys (Baker et al. 1997, 1999; Baker et al. 1997; Murthy and Fetz 1992; 1996) and humans (Baker 2007; Brown 2000; Conway et al. 1995; Halliday et al. 1998; Kilner et al. 2000; Kristeva-Feige et al. 2002; Kristeva et al. 2007; Riddle and Baker 2006; Salenius et al. 1997; Witte et al. 2007). During the last decade, beta-range coherence has been systematically investigated, and it was shown that it is task-dependent (Baker et al. 1999; Feige et al. 2000; Salenius et al. 1997), it reflects compliance (Kilner et al. 2000), displacement (Riddle and Baker 2006), attention (Kristeva-Feige et al. 2002), precision (Kristeva et al. 2007) as well as learning (Perez et al. 2006). Based on the finding that increased beta-range CMC and better performance are correlated we suggested the beta-range CMC as a mechanism for effective corticospinal interaction during static forces (Kristeva et al. 2007).

Since one of the main functions of the motor cortex is to control force output (Ashe 1997), modulation of the beta-range CMC by different static forces has been investigated, too. It was shown that while weak static forces are accompanied by beta-range CMC, submaximal and maximal forces are accompanied mainly by gamma-range CMC (Brown et al. 1998). During moderate contraction, these authors
showed co-existence of beta- and gamma-range (45-55 Hz) CMC. Brown et al. (1998) have suggested that gamma-range CMC is related to higher attentional involvement of the subject when producing submaximal and maximal forces. The force modulation of the CMC and especially the shift of the CMC from beta to gamma when the change is made from weak to maximal force was confirmed by Mima et al. (1999). Further, we provided evidence that beta-range CMC increases when compensating low-level static forces at 16%MVC instead of 4%MVC (Witte et al. 2007).

Schoffelen et al. (2005) showed that modulations of subjects' readiness to respond in a simple reaction-time task were closely correlated with the strength of gamma-range (40 to 70 Hz) CMC between motor cortex and spinal cord neurons. Corticomuscular gamma-range (30-45) coherence has also been associated by us with isometric compensation of low dynamic force (4%MVC) and may function to provide rapid integration of visual, cognitive (preparatory attention) and somatosensory information (Omlor et al. 2007). That “gamma rhythms accompany states of preparatory attention or vigilance” was demonstrated in modeling studies, too (Borgers et al. 2005). Furthermore, in Andrykiewicz et al. (2007), we have shown that during compensation of low-level dynamic modulated force at 4%MVC the gamma-range CMC is not modulated by the amplitude of the force.

We obtained these results in studies where either the force level of static forces (Witte et al. 2007), or the amplitude (but not the force level) of the dynamic modulated forces have been manipulated (Andrykiewicz et al. 2007). Therefore, it is still unknown to what extent these synchronization processes in the beta- and gamma-range are modified when only the force level (but not the amplitude) of a modulated force is increased. We addressed this question by applying a dynamic
force paradigm with different force levels, *i.e.* we manipulated only the force level while leaving the amplitude of the dynamic force unchanged. For this purpose, we investigated CMC during isometric compensation for dynamic modulated forces with three different force levels (8%MVC, 16%MVC and 24%MVC).

Omlor et al. (2007) and Andykiewicz et al. (2007) showed that high-beta and low gamma-range (30-45 Hz) CMC is observed during isometric compensation for dynamic forces. On the other hand, beta-range CMC during static force increases distinctly from 4%MVC to 16%MVC (Witte et al. 2007). These results suggest different functional roles of CMC in the two frequency ranges: the increase of force level is associated with larger beta-range CMC while the gamma-range (30-45 Hz) CMC allows rapid sensorimotor and cognitive integration during dynamic force output. Therefore, we predict that during isometric compensation of dynamic modulated force with increasing force level, we will observe CMC both in the beta- and gamma-range (hence a broad band coherence). In line with previous results, we also predict increasing CMC specifically within the beta range, while the gamma-range CMC remains unaltered.

The findings of this study confirmed these predictions, showing that for low-level dynamic forces (8%MVC, 16%MVC and 24%MVC) a strong broad band CMC peaking within the beta band is observed and it increases with the force level.
Materials and Methods

Subjects

Seven healthy right-handed female subjects (mean age 23.8 ± 3.1 years) without any history of neurological disease participated in the study. Handedness was tested according to the Oldfield questionnaire.

All subjects participated according to the declaration of Helsinki, with informed consent and the approval of the local ethics committee. None of the subjects had previously taken part in similar experiments.

Paradigm

During the experimental session, the subject sat in an electrically shielded, dimly lit room. The right arm was supported by a splint, and the subject was instructed to place the hand over a sphere and the right index finger in the ring of a home-made manipulandum (cf. Fig. 1 a).

(The please insert Figure 1 about here)

The manipulandum was designed for applying vertical forces on the finger, at the level of the metacarpophalangeal joint. A computer-controlled tooth belt drive produced a variable force on the ring. The force generated by the manipulandum was called target force. The subject had to compensate the force generated by the manipulandum isometrically to maintain the ring in its initial position. The force exerted by the subject was called exerted force. Visual feedback about the position of the ring was provided to the subject via a 19" monitor 120 cm in front of her with two
concentric circles. The green outer circle was fixed in the centre of the screen and represented the ring’s reference position while the white inner circle moved corresponding to the ring’s actual position. The subject had to maintain the small white circle inside the green circle at any time, so that when a given force was applied to the ring the subject had to apply the same force in the opposite direction (here flexion) to keep the ring in its initial position. The sensitivity of the visual feedback with respect to the finger position corresponded to 2.85 mm on the screen for 1 mm ring displacement. During the experiment, finger and ring were hidden from the field of view of the subject by a piece of cardboard.

Three different experimental conditions were investigated in a given recording session:

- **8% dynamic force condition:** During this condition, the manipulandum generated a sinusoidally modulated force at 8%MVC. The sine curve featured a frequency of 0.7 Hz and a peak-to-peak amplitude of 4%MVC (Fig. 1b).

- **16% dynamic force condition:** During this condition, the manipulandum generated a sinusoidally modulated force at 16%MVC force. The sine curve also featured a frequency of 0.7 Hz and a peak-to-peak amplitude of 4%MVC (Fig. 1b).

- **24% dynamic force condition:** During this condition, the manipulandum generated a sinusoidally modulated force at 24%MVC. The sine curve also featured a frequency of 0.7 Hz and a peak-to-peak amplitude of 4%MVC (Fig. 1b).
In all three conditions, the generated force had to be compensated isometrically. The MVC of the subject was measured prior to the beginning of the experiments. Note that this force compensation task is predictive and predictability is not manipulated among the three conditions.

To ensure a smooth start and end of the generated force by the manipulandum a rising cosine function was used. After the increase of the force in the trial to the given level, the subject had to compensate this force for about 12 s. The experimental session included 5 to 8 series of 30 trials (10 for each condition in a randomized order with 5 to 10 s rest period between them). The pauses between series lasted about 5 minutes. The subjects were instructed to avoid any other movements and to fix their gaze on the visual feedback during the task. The subjects were given some practice at the beginning of the study to get familiarized with the task.

**Recordings**

Electrical potentials (band-pass 0-200 Hz, sampling rate 1000 Hz) were recorded from 52 scalp positions according to the international 10-10 system (Synamp 2, NeuroScan, El Paso, TX, USA) referenced to Cz with ground at FzA. Electrode impedances were kept under 5 kOhm. The electrooculogram (EOG, same band-pass and sampling rate as for EEG) was recorded to exclude trials contaminated with eye movements from further analysis. Electromyographic activity (EMG, band-pass 5-200 Hz; sampling rate 1000 Hz) was recorded with surface electrodes using a belly-tendon montage from the pars indicis of the right flexor digitorum superficialis muscle, the prime mover of the index finger flexion.
Data analysis

Artifact rejection was visually performed off-line trial-by-trial to exclude segments contaminated with eye movements. To avoid transient effects, data related to the force ramp were not dealt with in this study. Continuous data of 10 s, in-between level triggered markers P1 and P2 (Fig. 1 b, c), were further divided into successive segments of 512 ms length, allowing for a frequency resolution of 1.96 Hz. The EEG signal was then transformed into the reference-free current source density distribution (CSD) which reflects the underlying cortical activity. The CSD algorithm was estimated using the spherical spline interpolation method implemented in the commercial software ‘BrainVision’ 1.05 (München, Germany). A total of 300 artifact-free segments were analyzed for each subject in each condition.

EMG signal was rectified, which is an appropriate procedure in power and coherence analysis (Myers et al. 2003; Yao et al. 2007) because it is known that full wave rectification provides the temporal pattern of grouped firing motor units. The discrete 512 points Fourier transform was calculated for each segment for the whole 1 to 500 Hz frequency range.

Calculation of the EEG spectral power (SP) and the EEG-EMG coherence

Power spectrum (SP) for a given channel \((c)\) was further calculated according to the following equation

\[
SP_c(f) = \frac{1}{n} \sum_{i=1}^{n} C_i(f) C_i^*(f)
\]

where \(C_i\) represents the Fourier transformed channel \(c\) for a given segment number \((i=1, \ldots, n)\) and \(^{*}\) indicates the complex conjugate.
Coherence values (Coh) were calculated between the rectified EMG and the EEG channels overlying the sensorimotor area contralateral to the active hand (SM1c) in order to calculate the synchronization between the two signals. Coherence values (Coh) were calculated on the basis of the following formulae:

\[
Coh_{c1,c2}(f) = \frac{|S_{c1,c2}(f)|^2}{SP_{c1}(f) \times |SP_{c2}(f)|}
\]

where

\[
S_{c1,c2}(f) = \frac{1}{n} \sum_{i=1}^{n} C1_i(f)C2_i^*(f)
\]

Thus \( Sc_{1,c2}(f) \) is the cross-spectrum for the EEG signal channel \( c1 \) and the rectified EMG signal in channel \( c2 \) at a given frequency \( f \) and \( SP_{c1}(f) \) and \( SP_{c2}(f) \) are the respective power spectra for \( c1 \) and \( c2 \) at the same frequency. For frequency \( f \), the coherence value, \( Coh(c1,c2)(f) \), thus corresponds to the squared magnitude of a complex correlation coefficient. \( Coh(c1,c2)(f) \) is then a real number between 0 and 1 (Mima & Hallett, 1999). This methodology for spectral and coherence analysis was used as implemented in the commercial software “Brain Vision 1.05” (MES, München, Germany).

Coherence is considered to be significant if the resulting value lies above the confidence level (CL)
where \( n \) is the number of segments and alpha, \( \alpha \), is the desired level of confidence (Halliday et al. 1995, Conway et al. 1995, Halliday et al. 1999). We considered coherence to be significant over the upper 95% confidence limit.

From all possible 52 scalp recordings we focused on the strongest coherences that were obtained between the EEG channels (C1 or C3) over the left sensorimotor area contralateral to the right index finger movement and the rectified EMG. This procedure may account for different location of the maximum CMC peak due to inter-individual differences in brain morphology.

**Statistical analysis of spectral power and coherence**

To test for any statistical difference on CMC and cortical power between the three different levels of dynamic force, we firstly measured the area under the coherence curve and above the significance level, \( A_{coh} \), and under the spectral power curve, \( A_{pow} \), in the 15-45 Hz frequency range (including the beta and gamma-range). Then, a separate analysis for only the gamma-range (30-45 Hz) was performed. For the EMG spectral power we took the 5-200 Hz frequency range.

In this kind of area (\( A_{coh} \)) analysis, it is reasonable to take the area under the curve of the coherence because it is a measure of the mean coherence within the considered frequency band (see Andrykiewicz et al. 2007; Omlor et al. 2007; Patino et al. 2008; Witte et al. 2007). This procedure is enough to make the case of a significant difference between the different conditions. Of course, it does not consider the
detailed variations of coherence for each frequency bin, but addresses the overall
effect within the frequency band of interest.

Afterwards the non-parametric Friedman test was applied to compare values $A_{coh}$
for CMC and $A_{pow}$ for SP measured in all three force conditions for each single
subject, with the null hypotheses that the distributions of the values tested are the
same across all three conditions. The Friedman test with the global null hypothesis
was calculated first to avoid an alpha-adjustment in the simultaneous paired
hypotheses. When the Friedman test indicated that not all of the three conditions
were statistically equivalent, we performed a second non-parametric test (paired
Wilcoxon test) on the resulting values $A_{coh}$ and $A_{pow}$. The null hypothesis was that the
difference between the matched samples of coherence and power spectra arises
from a distribution which is symmetric around zero. We applied this test to the
following condition pairs: 8%MVC and 16%MVC, 8%MVC and 24%MVC, 16%MVC
and 24%MVC.

There are currently several methods which have been developed to compare data
with considerable variances after stabilizing transforms. These transformations have
been widely used by others (Holliday et. al., 1995; Mima & Hallett, 1999) in order to
compare the coherence among different conditions by using parametric statistical
methods. However, these transformations are well suited when a parametric method
will be used for statistical comparison. In our case, we have not followed this
methodology, but used instead a non-parametric method (Friedmann test) to
compare statistically the three conditions, using the non-transformed coherence
values (area values). Another analysis depending on previous transformation of the
raw data was unnecessary.
In addition, to test a linear relationship between the CMC and the force level, we applied repeated ANOVA including an analysis of the polynomial contrast (linear and quadratic).

**Results**

*Corticomuscular coherence*

The maximum EEG-EMG coherences were observed over the contralateral motor cortex (C3 or C1). Figure 2a shows the grand average EEG-EMG coherence curves for the three force conditions (8%MVC, 16%MVC and 24%MVC). As seen from the figure there are significant broad-band coherences (over the 15 - 45 Hz range). For the 8%MVC condition, two separated cortico-muscular synchronization processes peaking in the beta (approx. at 22 Hz) and gamma (approx. at 35 Hz) range were observed in the 8% condition. On the other hand, for the 16%MVC and 24%MVC conditions, the CMC pattern shows a rather broader but single synchronization process peaking at approx. 22 Hz with “skirts” spreading down to ~15 Hz and up to ~40 Hz.

(Please, insert Figure 2 about here)

The CMC in this broad range increased significantly with the force level as seen from the grand averages (Fig. 2a) and from the individual coherence values (Fig. 2b) (Friedman test statistics 13.07; d.f.=2; p<0.002). The post hoc Wilcoxon signed rank test further revealed significant differences between 8%MVC (mean 0.069 ± 0.062) and 16%MVC (mean 0.159 ± 0.134) (Z=2.01, p<0.027), between 8%MVC and
24%MVC (mean 0.217 ± 0.165) (Z=2.37; p<0.018) and between 16%MVC and 24%MVC (Z=2.37; p<0.018).

The analysis of the polynomial contrast showed that the increment of the CMC over the 15-45 Hz range was mostly due to a linear effect (p=0.02), the quadratic part was not significant. Although the broad-band CMC was not suggestive of a separate synchronization process within the gamma band (30 - 45 Hz), we did a separate analysis of the gamma-range CMC and SP in order to compare these results with our previous ones. Gamma range CMC did not show significant differences between 8%MVC (mean 0.069 ± 0.055), 16%MVC (mean 0.088 ± 0.054) and 24%MVC (mean 0.106 ± 0.091). However, there was a tendency to increased CMC values as seen from the grand averages (Fig. 2a).

**Cortical motor spectral power**

We determined the cortical motor power over the contralateral left motor cortex. The grand average for the SP and the individual values in the 15-45 Hz frequency range are shown in Figure 2c and 2d respectively. The SP did not correlate with the increasing modulated force level. A separate analysis of the gamma-range SP did not show any statistical modulation of the SP with the force level.

**EMG spectral power**

No significant differences between the EMG spectral powers among the different force conditions were observed.

**Discussion**

*Modulation of CMC in the 15-45 Hz range*
The present study was designed to investigate how the CMC in the 15-45 Hz range (beta- and gamma-range) behave during isometric compensation of an increasing modulated force in the low force range (8%MVC - 24%MVC). The findings show a broad-band (15-45 Hz) CMC comprising both beta- and gamma-range peaking within the beta-range (approx. at 22 Hz). This broad-band CMC increases significantly with the force level (Fig. 2b).

Is there a separate synchronization process within the gamma-range?

The pattern of beta- and gamma-range CMC was different for the three conditions. In line with our previous work, two clearly separated cortico-muscular synchronization processes peaking in beta- (approx. at 22 Hz) and gamma-range (approx. at 35 Hz) were observed in the 8%MVC condition only (Fig 2a). This suggests functional coexistence of two different processes within the corticospinal circuit. On the contrary, for 16%MVC and 24%MVC conditions, broad-band coherences (15-45 Hz) peaking within the beta-range were obtained, so that a clear differentiation of two synchronization processes in beta- and gamma-range was not observed.

Therefore, our data is more consistent with a unique CMC process located within the beta-range with broad “skirts”. The amplitude of this beta-range CMC correlates linearly with the modulated force level. A separate gamma-range synchronization process, although observed for the lowest force level (8%MVC condition) and predicted on the basis of our previous findings (Andrykiewicz et al. 2007; Omlor et al. 2007) could not be consistently demonstrated in this study. Therefore, we have been unable to show the functional specificity of gamma-band CMC to dynamic force output. It remains a topic of future studies (e.g. using intracortical recording) to
elucidate if separate gamma-band CMC coexists with beta-band CMC for increasing force level of dynamic modulated forces.

Beta-range CMC is not specific to isometric compensation for static forces

Our previous finding about higher beta-range CMC when the static force level is increased from 4%MVC to 16%MVC (Witte et al. 2007) is extended here for isometric compensation of increased modulated force. Witte et al. (2007) suggested that beta-CMC may serve to stabilize corticospinal communication during isometric compensation of low-level static forces. Our results favour the view that this function of beta-CMC is not confined to or specific for low-level static forces only. Rather, the sensorimotor system may resort to stronger and also broader beta-range CMC to generate stable corticospinal interaction during increasing force level, even when compensating for dynamic modulated forces.

Cortical motor spectral power

Surprisingly, we did not find any significant modulation either of the beta- or of the gamma-range spectral power among the different force levels of the dynamic force. With regard to the gamma-range this result is in agreement with the former studies which have reported relative independency of gamma-CMC and cortical motor spectral power in the gamma-range (Omlor et al. 2007; Schoffelen et al. 2005). Concerning the beta-range this result was unexpected since we have provided evidence for a positive correlation between beta-range CMC and cortical motor spectral power in the beta-range (Kristeva et al. 2007). On the other hand, elevated spectral power in the beta-band has been associated with decreased cortical
excitability (Chen et al. 1999), whereas decreased cortical motor beta-power is known to correspond to motor acts demanding high-level attention (Chen et al. 2003; Jantzen et al. 2001). Even at the force level 24%MVC, this force condition still requires rapid recalibration of motor programs, high-level attention and thereby dynamic cortical processing – a state which may be incompatible with increased beta-synchronization of cortical motor cell assemblies despite the elevated beta-range CMC. Further evidence that beta-range CMC and cortical motor beta-power are not always positively correlated comes from a study of Baker et al. (2003), in which the authors amplified the beta-power through a diazepam-injection but did not observe a simultaneous increase of the beta-range CMC.

Functional role of beta- and gamma-range CMC

Synchronization processes have shown a pervasive presence in the CNS at several levels of neuronal organization and for different cognitive processes (Engel et al. 2001). A detailed understanding of the functional roles of CMC for different frequency ranges would represent a major advance in motor control. A thorough examination of the findings reported until now suggests multiple functions rather than specific functional roles for specific frequency ranges. This is in line with a one-to-many relationship where corticomuscular synchronization in one frequency-range may be involved in different functions and vice versa. For instance, coexistence of MEG-EMG coherence in the beta- and gamma-range has been reported during medium (50-60%MVC) static contraction by Brown et al. (1998). Marsden et al. (2000) measured ECoG-EMG-coherence in the beta- and gamma-range during high-level static forces and phasic movements respectively. Our previous work has contributed to this debate showing that beta- and gamma-range CMC are observed during
isometric compensation of low-level static and dynamic forces respectively (Omlor et al. 2007). Our present findings further support the multiple functions of one and the same frequency range, showing that broad-band beta-range CMC positively correlates with the level of a dynamic (modulated) force.

We therefore suggest that CMC is a highly dynamic synchronization process with multiple functions and involve either specific beta- and gamma subranges or broad frequency ranges according to the specificities of the motor task. However, the different corticospinal circuits associated to these different CMC patterns cannot be easily differentiated in non-invasive recordings such as EEG or MEG due to spatial smearing of neighbour neural fields (Nunez and Srinivasan 2006; Schoffelen et al. 2008).

Conclusions

Our study shows a broad-band (15-45 Hz) beta-range CMC during isometric compensation of a modulated force. The CMC amplitude positively correlates with increasing force level. Our results favour the view that the function of beta-range CMC is not specific for low-level static forces only. The sensorimotor system may resort to stronger and also broader beta-range CMC to generate stable corticospinal interaction during increased force level, as well as when compensating for dynamic modulated forces.

This finding re-enforces the importance of the beta-range EEG-EMG coherence in sensorimotor integration.

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Figures

Figure 1. (a) Manipulandum and hand position during the experimental paradigm. (b) Superimposed force profiles generated by the manipulandum in the three different conditions (8%MVC, 16%MVC and 24%MVC). P1 and P2 are the start and end markers for further analysis (c) Performance (Position Error) of one subject for the three different conditions. Note that the force level and the Position Errors increase from 8%MVC (dotted line) to 16%MVC (thin line) to 24%MVC (thick line).

Figure 2. EEG-EMG coherence between the left sensorimotor area and the right FDI muscle for 8%MVC, 16%MVC and 24%MVC. (a) Grand-average EEG–EMG coherence in the 4-45 Hz range. The confidence level at 95% is marked with a horizontal line. Note that the coherence values increase from 8%MVC (dotted line) to 16%MVC (thin line) to 24%MVC (thick line). (b) Individual CMC (area values) for the 7 subjects in the 15-45 Hz range. Note that the coherence values increase linearly from 8%MVC to 16%MVC to 24%MVC. (c) Grand-average EEG Spectral Power in the range from 4-45 Hz. (d) Individual EEG Spectral Power (area values) for the 7 subjects in the 15-45 Hz range. Empty circles correspond to 8%MVC condition, filled gray circles to 16%MVC condition and filled dark circles to 24%MVC condition. Squares represent the Grand-average values, and code the three different conditions using the same convention as for the circles.