Corticomuscular Coherence Reflects Interindividual Differences in the State of the Corticomuscular Network During Low-Level Static and Dynamic Forces

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Introduction

There have been many studies of beta-range synchronization between cortical motor areas and muscles as measured by corticomuscular coherence (CMC) during the control of static forces (SFs) (Murthy and Fetz 1992, 1996a, 1996b; Sanes and Donoghue 1993; Conway et al. 1995; Baker et al. 1997). CMC has been shown to be both task and force dependent and related to attention, compliance, displacement, fatigue, and age (Kristeva-Feige et al. 1993; Conway et al. 1995; Murthy and Fetz 1996a; Salenius et al. 1997; Halliday et al. 1998; Brown 2000; Feige et al. 2000; Gross et al. 2000; Baker MR and Baker SN 2003; Baker et al. 2006; Perez et al. 2006; Riddle and Baker 2006; Tecchio et al. 2006; Witham et al. 2010). Beta-range cortical motor spectral power (SP) and CMC during isometric compensation for SFs has been suggested as a mechanism for effective corticospinal interaction, which subserves different functions (Baker et al. 1999; Kristeva et al. 2007). Furthermore, when low-level predictable DFs have to be isometrically compensated instead of static ones, the corticospinal oscillatory mode shifts toward a low gamma subrange (30–45 Hz). This gamma-subrange is predominantly engaged in binding proprioceptive, visual feedback, and cognitive (preparatory attention) information to ensure an appropriate motor response (Andrykiewicz et al. 2007; Omlor et al. 2007; Patino et al. 2008).

In the investigation of corticomuscular coherence (CMC), it remained unclear why some subjects do not present significant CMC. We predicted that such subjects will develop CMC as a result of learning as indexed by improved performance during a visuomotor task. We investigated CMC, cortical motor spectral power (SP), and performance in 14 subjects during isometric compensation of a static force or dynamic force (DF) with their right index finger. We compared data from the beginning of the experiment (Time-Period 1) and after learning (Time-Period 2). Eight subjects (Group CMC+++) presented CMC during Period 1 which increased during Period 2. Six subjects (Group CMC++-) presented CMC only during Period 1. Group CMC-- was "more desynchronized" (lower SP, and stronger task-related desynchronization) than Group CMC+++. The performance was better in Group CMC+++ than in Group CMC--. Learning was associated with higher SP, higher CMC, and better performance in both groups. However, in the more complicated DF condition, Group CMC+++ learned better than Group CMC--. The present study demonstrates the presence of CMC in all subjects tested and evidence that this is due to the fact that individuals may fall into 2 different groups in terms of oscillatory motor control: Group CMC+++ presents CMC only after learning.

Keywords: coherence, corticomuscular, EEG, force, human
To better characterize the state of the cortical motor network for the 2 groups with and without CMC, we used the event-related desynchronization (ERD): Increased cellular excitability in thalamocortical systems results in a low-amplitude desynchronized EEG (Steriade and Llinás 1988). Therefore, the amount of the cortical activation during a sensory, motor, or cognitive task could be indexed by the ERD or TRD with reference to a baseline (Pfurtscheller and Aranibar 1977; Pfurtscheller 1992; Pfurtscheller and Andrew 1999). Based on these and on the above mentioned results of Baker et al. (1999) and Kristeva et al. (2007), we further predicted that the subjects without CMC before learning will be more desynchronized, that is, they will have stronger TRD than the subjects showing CMC.

The findings confirmed our predictions. Moreover, because the group without CMC before learning showed stronger TRD (i.e., stronger cortical activation) for the same performance as the group presenting CMC, we suggested that individuals fall into 2 groups in terms of oscillatory motor control: those with higher and those with lower cortical "motor efficiency." We defined the cortical motor efficiency as cortical activation as reflected in the TRD for the same performance. Subjects with lower motor efficiency need stronger cortical activation for the same performance as the subjects with higher motor efficiency.

**Materials and Methods**

**Subjects**

Fourteen healthy right-handed subjects (female, mean age 28.2 ± 11.3 years) without any history of neurological disease took part in the study. To exclude cyclic ovarian effects on the cortical excitability and oscillatory cortical activity, the female subjects were in different lunar phases (Smith et al. 2002). The handedness was tested according to the Oldfield questionnaire (Oldfield 1971). Three of the subjects had already participated in similar experiments.

All subjects participated according to the declaration of Helsinki, with understanding and informed consent of each subject and approval of the local ethics committee.

**Experimental 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 custom-built manipulandum (Fig. 1A).

The manipulandum was designed for applying vertical forces on the finger at the level of the metacarpophalangeal joint. A computer-controlled tooth belt drive with 2 sensors to measure vertical forces and displacements produced a defined force on the ring of the manipulandum. This force was called target force. The subject had to compensate isometrically the target force generated by the manipulandum and to maintain the ring of the manipulandum in its initial position (Fig. 1A).

Visual feedback about the position of the ring was provided to the subject via a 19" monitor placed 100 cm in front of her with 2 concentric circles (Fig. 1B). The green outer circle (radius 6 mm including the thickness of 2 mm) was fix and represented the ring's reference position, while the inner solid white circle (radius 2 mm) moved corresponding to the ring's actual position. The subject had to maintain the small white circle inside the green circle, so that when a target force was applied to the ring of the manipulandum, the subject had then to compensate it by applying a force in the opposite direction (here flexion) to keep the ring of the manipulandum in its central position. A finger displacement of 1 mm corresponded to 2.85 mm visual feedback. The tolerance for the positional errors was the green circle. Parts of the trials in which the white circle exited the green circle were excluded from further analysis.

During the experiment, the manipulandum generated a target force at 8% of the maximum voluntary contraction (MVC), which was determined prior to the experiment (Fig. 1C). We used such low force because it was shown that the motor cortical neurons are most sensitive to forces within a low force range (Hepp-Reymond et al. 1989). The target force of 8% MVC had to be compensated first in static and after that in dynamic fashion. Thus, one trial of the "target force" had 4 different phases (Fig. 1C): a "ramp phase" (rising cosine function to ensure a smooth start. The 1 s ramp phase was followed by 8-s period of "static force" (SF, between markers T1 and T2). The SF was followed by DF (between markers T2 and T3). The DF was sinusoidally modulated with frequency of 0.66 Hz and 8% MVC peak-to-peak amplitude. It lasted 9 s instead of 8 s to allow a complete end of a sinusaloid cycle. The DF was followed by downward ramp phase (again cosine function) to ensure a smooth end of the generated force. The tolerance for the positional errors was the same for the SF and DF.

**Figure 1.** Experimental setup. (A) High-resolution EEG recorded from 62 scalp positions together with electrooculogram, home-made manipulandum, and EMG recorded from FDI, FDS, and EDC muscles during the experiment. (B) Visual feedback of the ring position displayed on a monitor in front of the subject. The position values of the borders of the outer fixed green circle are at ±6.1 mm. (C) Target force profile: SF in black and DF in gray. The SF and DF are at 8% MVC. The DF represents a periodically modulated sinusoidal wave at frequency 0.66 Hz and peak-to-peak amplitude of ±8% MVC. T1-T2 and T2-T3 are the intervals considered for the data analysis for SF and DF, respectively. (D) Grand average finger position.
Prior to the experiment, we recorded rest EEG for 5 min while subjects were attending at the small white circle and their right hand was resting over the sphere with the right index finger in the ring of the manipulandum. During this rest period, no force was applied by the manipulandum. After that the force corresponding to the individual MVC was measured. Then subjects performed a few trials to get familiarized with the task and to learn "what" to do and "how" to do. The experiment started after the task was learned. Therefore, we investigated rather the effect of motor adaptation, which is also a part of motor learning.

The experimental session consisted of 15 recording series, while each series included 10 trials. To avoid attentional variations across trials, in 1 of the 10 trials the order of the SF and DF was reversed: in these trials called "opposite" trials, the subject had to maintain the target force first in dynamic and after that in static fashion. The opposite trials occurred pseudorandomly in the series. After each trial, the subject had to report verbally whether the trial was static-dynamic or dynamic-static. The opposite trials were included only to avoid attentional variations across trials. They were excluded from further analysis.

To avoid muscle fatigue, rest intervals of random duration of 5-10 s were included between the trials and approximately 5 min between the series.

The subjects were instructed to avoid any other movements and to fix their gaze on the visual feedback during the experiment.

**Recordings**

The EEG (bandpass DC-200 Hz, sampling rate 1000 Hz) was recorded from 62 scalp positions referenced to Cz with ground at FzA, according to the 10/10 system (SynAmps 2, NeuroScan, El Paso, TX) (Fig. 1A). Electrode impedances were kept under 5 Kohm. The electrooculogram (same bandpass and sampling rate as for EEG) was recorded to exclude trials contaminated with eye movements for further analysis. Electromyographic activity (EMG, bandpass DC-200 Hz; sampling rate 1000 Hz) was recorded with surface electrodes using a belly-tendon montage from 3 muscles: pars indicis of the right flexor digitorum superficialis (FDS), the right first dorsal interosseus (FDI), and the right extensor digitorum communis (EDC). In our task, which is co-contraction, the 3 muscles are synergetic and their cortical representations are intermingled (Spinks et al. 2008). The set point of the force and displacement of the finger were recorded in parallel with the electrophysiological data (same bandpass and sampling rate as for EEG). Data were stored and analyzed off-line.

**Data Analysis**

**EEG-EMG Coherence Analysis**

To avoid transient effects, data related to the force ramp phases were not dealt with in this study. Trials where the position error (PE) exceeded the tolerance for the positional error was excluded from further analysis.

Only data between markers T1 and T2 was included for further analysis. In each trial, data between markers T1 and T2 was first separated in 2 data sets corresponding to SF (between the markers T1 and T2) and to DF (between the markers T2 and T3) (Fig. 1C). Data belonging to SF from all trials were concatenated. The same was done for data belonging to DF. Then, for both SF and DF, data were further cut into nonoverlapping segments. Segments had duration of 512 ms, therefore allowing a frequency resolution of 1.96 Hz for further spectral analysis. Artifact rejection was visually performed off-line trial by trial to exclude segments contaminated with eye movements. The EEG signal was then transformed into the reference-free current source density (CSD) distribution that reflects the underlying cortical activity (Nunez et al. 1997). The CSD algorithm was estimated using the spherical spline interpolation method (Perrin et al. 1989) implemented in the commercial software "Brain Vision 2.0.1" (München, Germany). For each subject, sequences of 300 segments were averaged for both SF and DF. Thus, for each of the 300 segments, we had values for SP, CMC, PE, and TRD.

For each subject, we compared the SP, the CMC, PE, and TRD values between Time-Period 1 and Time-Period 2. Period 1 consisted of the first 300 segments (duration of 512 ms each) of the experimental session. Period 2 consisted also of 300 segments (duration of 512 ms each) from a later time period of the experimental session when the highest CMC occurred. Thus, Period 1 was before learning and Period 2 after learning. Across subjects values for SP, CMC, PE, and TRD belonging to Period 1 and Period 2 were pooled separately.

EMG signals were rectified as it is known that full-wave rectification, which provides the temporal pattern of grouped firing motor units (Halliday et al. 1995), is an appropriate procedure for power and coherence analysis (Yao et al. 2007). The discrete 512 points Fourier transform was computed for each segment for the whole 0-200 Hz frequency range.

**Calculation of EEG and EMG SP and EEG-EMG Coherence (CMC)**

SP for a given channel (c) was further calculated according to the following formula:

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

(1)

where $C_i(f)$ represents the Fourier transformed channel $c$ for a given segment number ($i = 1, \ldots, n$) and $^*$ indicates the complex conjugate.

Coherence values 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 2 signals. Coherence values were calculated on the basis of the following formula:

$$Coh_{1,2} \left( f \right) = \frac{|S_{1,2}(f)|^2}{SP_{1}(f) SP_{2}(f)}$$  

(2)

thus, $S_{1,2}(f)$ is the cross-spectrum for the EEG signal channel c1 and the rectified EMG signal in channel c2 at a given frequency $f$, $SP_{1}(f)$ and $SP_{2}(f)$ are the respective spectral power for $c1$ and $c2$ at the same frequency. For frequency $f$, the coherence value, $Coh_{1,2}(f)$, thus corresponds to the squared magnitude of a complex correlation coefficient. The function $Coh_{1,2}(f)$ is a real number between 0 and 1. Coherence is considered to be significant if the resulting value lies above the confidence level (Rosenberg et al. 1989)

$$CL_5(\gamma) = 1 - (1 - \gamma)^5,$$

(4)

where $n$ is the number of segments and $s$ is the desired level of confidence. We considered coherence to be significant above the 95% confidence limit.

We focused on the strongest coherences obtained between the EEG channels (C1 or C3) over the left sensorimotor area contralateral to the active right index finger movement and the rectified EMG. This procedure may account for the different location of the maximum CMC peak (C1 or C3) due to interindividual differences in brain morphology.

**Analysis of Center of Gravity**

To detect frequency shifts within the coherence spectrum, we also calculated the Center of Gravity (CoG) for the frequency (CoGf), that is, the frequency at which all CMC activity could in theory be concentrated; around this point the CMC is balanced. This was done according to

$$CoG_f = \frac{\sum_{i=1}^{n} f_i \times Coh_i}{\sum_{i=1}^{n} Coh_i},$$

(5)

where $i = 1, \ldots, n$, indicates the number of significant bins with its respective frequency value $f$ and coherence amplitude $Coh$.

For the coherence values, the individual means were calculated according to
We defined the TRD as previously filtered the EEG in the range 10-12 Hz with a slope of 48 dB/decade (Pfurtscheller and Lopes da Silva 1999). To perform such analysis, we analyzed the desynchronization in the alpha-range using a variant of the TRD in each subject, we calculated the areas under the curves in the alpha range (8-12 Hz).

Calculation of the TRD

The amount of cortical activation during SF and DF was quantified by the SP decrease at the channel of the maximum CMC which was in all subjects C3 of the high-frequency (8-12 Hz) alpha rhythm with reference to a baseline period as described in Babiloni et al. (2004). We analyzed the desynchronization in the alpha-range using a variant of the well-known method of TRD (Pfurtscheller and Aranibar 1977; Pfurtscheller and Lopes da Silva 1999). To perform such analysis, we previously filtered the EEG in the range 10-12 Hz with a slope of 48 dB/decade, and then we defined the TRD as

\[
TRD = \left( \frac{SP_{null} - SP_{Rest}}{SP_{null}} \right) \times 100,
\]

where \( SP_{null} \) is the SP of the EEG were significant CMC was calculated (during SF or DF) and \( SP_{Rest} \) is the SP of the baseline EEG. To quantify the TRD in each subject, we calculated the areas under the curves in the alpha range (8-12 Hz).

Statistical Analysis

Corticomuscular Coherence

To test for any statistical difference in CMC, we measured the area under the coherence curve and above the significance level, \( A_{coh} \). The frequency window for \( A_{coh} \) was 5-15 Hz.

To compare values for the \( C_{coh} \) and \( A_{coh} \) for all 14 subjects between SF and DF, we performed Wilcoxon signed-rank test with the null hypotheses that the differences of the means for SF and DF are zero.

Statistical Analysis of the Cortical Motor SP

To test for any statistical difference in the cortical motor SP, we measured the area under the SP curve, \( A_{power} \). The frequency windows for EEG \( A_{power} \) were 7-14 Hz (alpha), 15-30 Hz (beta), and 31-45 Hz (gamma).

For the statistics of the SP in the different frequency windows, individual values for \( A_{power} \) for EEG were first transformed logarithmically to yield symmetric distributions according to the formula:

\[
A’_{power} = \log_{10}(1 + A_{power}).
\]

Performance (PE)

To account for the intersubject variability and to render the distribution symmetric, the PE values were first logarithmically transformed

\[
PE = \log_{10}(0.01 + PE) + 2.
\]

MANOVA and ANOVA

At the beginning of the experiment, during Period 1, 8 subjects (Group CMC++) showed CMC and the other 6 subjects (Group CMC+) did not present CMC. The absence of CMC was defined as CMC values below the significance level.

After the preparation of CMC (\( A_{coh} \)), SP (alpha \( A’_{power} \), beta \( A’_{power} \), gamma \( A’_{power} \)), and PE (PE) data, we first performed multivariate analysis of variance (MANOVA) to investigate the multivariate effects. After that a repeated measure 3-way analysis of variance (ANOVA) was performed under the null hypothesis that the dependent variables were the same across the 3 factors: The between-subject factor Group (Group CMC++ and Group CMC–), and 2 intraindividual factors: Force Condition (SF, DF), and Period (Period 1 and Period 2).

To highlight the group differences in performance as defined by PE in addition to the 3-way ANOVA, a Mann-Whitney test was performed.

Statistical Analysis of TRD

Individual values for \( A_{TRD} \) were first transformed logarithmically to yield symmetric distributions according to the formula:

\[
A’_{TRD} = \log_{10}(1 + A_{TRD}).
\]

With the values of the areas of each individual’s TRD, we estimated the modulation of the cortical activation using a 3-way ANOVA with the following factors: Group (Group CMC++, Group CMC–), Force (static, dynamic, Period (Period 1, Period 2).

Statistical Analysis of Correlations

Whenever the ANOVA indicated a significant beta and alpha SP increase, we calculated the Spearman correlation coefficients between both. The significance of correlations was calculated 2-tailed.

Results

All subjects performed the task according to the instructions. None of them reported fatigue or anxiety during the experimental session. All of them reported that they have learned the task and performed better later during the experiment.

Figure 1D shows the grand average of the finger position for the 14 subjects (150 trials for each participant). The frequency of the oscillations corresponded to the target force frequency 0.66 Hz.

Corticomuscular Coherence

Eight of the 14 subjects investigated presented CMC already during the Period 1 (Group CMC++: S4, S5, S6, S7, S10, S11, S12, and S13). The other 6 subjects did not present significant CMC during Period 1 but developed such after learning during Period 2 (Group CMC+: S1, S2, S3, S8, S9, and S14).

For all subjects, the strongest CMC occurred over the left sensorimotor cortex particularly at C3 with the FDI (9/14), FDS (2/14), and EDC (3/14). As far as the muscles to which the strongest CMCs occurred, no Group differences were found. In both groups, the strongest CMCs were to FDI (Group CMC++: 6/8 and Group CMC+: 4/6).

The main difference between SF and DF in our study was that the SF was accompanied by beta-range (15-30 Hz) CMC and the DF by low gamma-range (30-45 Hz) CMC. The beta-range CMC was broad banded (11.6 ± 1.7 Hz), and the gamma range CMC was narrow banded (3.4 ± 0.58 Hz).

Figure 2 shows original curves of CMC for both SF (black line) and DF (gray line) of some representative subjects from the Period 1 in Group CMC++ and from Period 2 in Group CMC+. All but one (S7) presented gamma-range CMC during DF. There were interindividual differences in the frequency of the beta-
range CMC: Subjects 2 and 3 (right panel in Fig. 2) showed beta-range CMC at low beta-range (8–22Hz).

When the results were pooled for all subjects, the following picture occurred; the beta-range CMC had mean frequency of $23.3 \pm 4.8$ Hz and mean amplitude of $0.07 \pm 0.04$. The gamma-range CMC had maximum amplitude of $0.02 \pm 0.007$ and mean frequency of $36.1 \pm 4.5$ Hz. Overall, the beta-range CMC was absent during DF. Only Subject 7 presented diminished beta-range CMC during DF.

To better visualize the shift of the frequency of the CMC toward higher frequencies from SF to DF, we calculated the individual CoG of the coherent activation ($\text{CoG}_f$) of CMC (Fig. 3, x-axis). Analogously to visualize the decrease of CMC from SF to DF, we calculated the individual mean coherence ($\text{Meancoh}$) (Fig. 3, y-axis). Indeed, in all subjects (only S7 was an exception), the $\text{CoG}_f$ from SF to DF was shifted to higher gamma frequencies. The extent of the frequency shift varied between 12 and 42 Hz. This shift was statistically significant ($P < 0.0001$, Wilcoxon paired test $n = 14$) and present in both Groups (Group CMC++: $P < 0.04$, $n = 6$ and Group CMC+: $P < 0.02$, $n = 8$).

As seen from Figures 2 and 3, one of the subjects (S7) showed beta-range CMC for both SF and DF. However, the amplitude of the beta-range CMC for this subject during DF was considerably reduced.

**Modulation of the CMC, Alpha SP, Beta SP, Gamma SP, and Performance (PE) by the Following factors: Group, Period, and Force**

Figure 4 shows the grand average of CMC curves, grand average of SP curves, and the logarithmic error position (log EP) for both groups for SF during Period 1 (before learning) and during Period 2 (after learning). Figure 5 shows the same for DF. In these figures, the qualitative group differences are very clear, especially that Group CMC+ does not present CMC before but presents such after learning, that the SP during SF is lower in Group CMC++ than in Group CMC++ for both before and after learning and that after learning, there is SP and CMC increase for both SF and DF. In addition, the performance is better during Period 2, that is, after learning.
Table 1 shows the results of the 2(P1, P2) 2(SF, DF) 2(G1, G2) design MANOVA for all 5 variables together (CMC, alpha SP, beta SP, gamma SP, and PE). The MANOVA with repeated measurements revealed highly significant multivariate effects for all factors and interactions but no effect of the Period Group interaction.

Table 2 shows the results of the 3-way ANOVA for each of the 5 variables separately:

The 3-way ANOVA for CMC revealed significant main effects for the following factors: Period (within-subject, Period 1 and Period 2, i.e., before and after learning), Force (within-subject, SF and DF), and Group (between-subjects, Group CMC++ and Group CMC—) (see Table 2, CMC). Significant were also the Force 3 Group and Period 3 Force interactions effects.

The outcome of the statistical analysis speaks in favor of clear increase of the CMC after learning for both Force conditions and for both groups. Furthermore, the CMC is higher during SF than during DF.

The 3-way ANOVA for alpha-range SP revealed significant main effects for the following factors: Period, Force, and Group (cf. Table 2 [alpha SP] and Figs 4 and 5). The statistical analysis disclosed higher alpha SP after learning for both groups, higher alpha SP for SF than for DF. There are overall significant group differences with higher alpha SP in Group CMC++. The 3-way ANOVA for beta-range SP revealed significant main effects for the following factors: Period, Force, and Group. Significant were also the Force 3 Group, Period 3 Force, and
Corticomuscular Coherence during Isometric Forces

The significant P_EP_Gamma SP_Beta SP (Spearman–Rho correlation coefficient 0.727, significantly correlated with the alpha SP increase after learning. correlations showed that the beta SP increase after learning is the statistical analysis revealed lower PE after learning, and significant correlations were not present in Group CMC.

Analysis of the Performance as Reflected in the PE

Thus, the outcome of the statistical analysis revealed stronger cortical activation for both groups during dynamic than during SF, stronger cortical activation for both Groups during Period 1, that is, before learning. Furthermore, the cortical activation was stronger for Group CMC+ than for Group CMC++ before and after learning for both force conditions.

However, the cortical SP during rest did not show differences between both groups.

Discussion

It has been reported that CMC is highly variable across subjects with absence of significant CMC in many subjects. To our knowledge, the present study demonstrates for the first time the presence of CMC in all subjects tested and evidence that this can be achieved taking into account learning effects over the duration of the experiment. As stated in the Materials and Methods, we use the term learning for simplicity only. Actually, we investigated the effects of motor adaptation because the actual learning of what and how to do was prior to the experiment. During motor adaptation, which also represents a kind of learning the motor system constantly uses relevant error information to improve performance. Specifically, we found that individual subjects fell into 2 different groups in terms of oscillatory motor control: those with higher and those with lower cortical motor efficiency. We defined the cortical motor efficiency as cortical activation as reflected in the TRD for the same performance. Subjects with lower “motor efficiency” need stronger cortical activation for the same performance as the subjects with higher motor efficiency. Subjects with lower motor efficiency do not present CMC at

### Table 2

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<tr>
<td>Beta SP Group</td>
<td>156.64</td>
<td>1</td>
<td>12</td>
<td>&lt;0.001</td>
<td>0.929</td>
</tr>
<tr>
<td>Beta SP Period</td>
<td>18.47</td>
<td>1</td>
<td>12</td>
<td>&lt;0.001</td>
<td>0.851</td>
</tr>
<tr>
<td>Beta SP Group × Period</td>
<td>1.29</td>
<td>1</td>
<td>12</td>
<td>0.278</td>
<td>0.097</td>
</tr>
<tr>
<td>Force</td>
<td>11.95</td>
<td>1</td>
<td>12</td>
<td>0.005</td>
<td>0.499</td>
</tr>
<tr>
<td>Gamma SP Force × Group</td>
<td>0.89</td>
<td>1</td>
<td>12</td>
<td>0.363</td>
<td>0.069</td>
</tr>
<tr>
<td>Gamma SP Period</td>
<td>1.93</td>
<td>1</td>
<td>12</td>
<td>0.190</td>
<td>0.138</td>
</tr>
<tr>
<td>Gamma SP Force × Group</td>
<td>0.00</td>
<td>1</td>
<td>12</td>
<td>0.996</td>
<td>0.000</td>
</tr>
<tr>
<td>Gamma SP Group</td>
<td>0.20</td>
<td>1</td>
<td>12</td>
<td>0.660</td>
<td>0.017</td>
</tr>
<tr>
<td>Gamma SP Period</td>
<td>69.66</td>
<td>1</td>
<td>12</td>
<td>&lt;0.001</td>
<td>0.851</td>
</tr>
<tr>
<td>Gamma SP Group × Period</td>
<td>2.12</td>
<td>1</td>
<td>12</td>
<td>0.171</td>
<td>0.150</td>
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<tr>
<td>Force</td>
<td>48.68</td>
<td>1</td>
<td>12</td>
<td>&lt;0.001</td>
<td>0.802</td>
</tr>
<tr>
<td>EP Force × Group</td>
<td>0.09</td>
<td>1</td>
<td>12</td>
<td>0.767</td>
<td>0.008</td>
</tr>
<tr>
<td>EP Force × Period</td>
<td>10.37</td>
<td>1</td>
<td>12</td>
<td>0.007</td>
<td>0.464</td>
</tr>
<tr>
<td>EP Force × Group × Period</td>
<td>2.20</td>
<td>1</td>
<td>12</td>
<td>0.163</td>
<td>0.155</td>
</tr>
<tr>
<td>Group</td>
<td>8.18</td>
<td>1</td>
<td>12</td>
<td>0.014</td>
<td>0.405</td>
</tr>
</tbody>
</table>

The significant P values are in bold.
the beginning of the experiment but do so after some period of
time that can be attributed to motor adaptation effects.
Furthermore, in the more complicated DF condition, only the
group with higher motor efficiency showed learning effects as
indexed by better performance.

Motor Adaptation Is Associated with Higher Cortical
Motor and Corticomuscular Synchrony

Higher CMC values were shown to occur with fatigue (Tecchio
et al. 2006). However, significantly better performance after
motor adaptation in our study suggests an alternative in-
terpretation for changes in CMC over time and favors motor
adaptation effects.

During SF, the increased cortical motor synchrony as
reflected in the higher SP after motor adaptation was strongest
for beta-range for both groups of subjects. As predicted, the
beta SP increases were associated with higher corticomuscu-
lar coherence. Learning during DF was again associated with
higher cortical motor synchrony and higher CMC.

The synchronous discharge of the neurons in the primary
motor cortex shown by Allum et al. (1982), Baker et al. (1999),
and Hatsopoulos et al. (1998) may be more effective in driving
spinal motoneurons (Baker et al. 1999; Kristeva et al. 2007). The
higher alpha- and beta-range synchrony after learning in the
group, which did not present CMC at the beginning of the
experiment, is related to the occurrence of CMC. Higher alpha-
and beta-range synchrony after learning were found as well as in
Group CMC++ which was from the very beginning “more
synchronized” with alpha- and beta-range synchrony peaks very
similar to those of Group CMC– during Period 2. This means that
in both groups, learning is associated with stronger beta-range
synchrony and higher CMC. The higher beta-range SP in Group
CMC+ can be related to more efficient sensorimotor processing
or perhaps more focused attention (Fisher et al. 2002;
Kristeva-Feige et al. 2002; Kilner et al. 2004; Baker 2007; Lalo et al.
2007) Pogosyan. In line with our previous results (Kristeva et al.
2007) is also the significantly higher alpha SP after learning. It is
very interesting that only in Group CMC– during Period 2. This means
that during Period 2, that is, after learning the TRD is lower. Note also the stronger TRD during DF than during SF.

Table 3
Results from ANOVA for TRD

<table>
<thead>
<tr>
<th>Factors</th>
<th>$F$</th>
<th>$df_1$</th>
<th>$df_2$</th>
<th>Significance</th>
<th>Partial $\eta^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Period</td>
<td>62.72</td>
<td>1</td>
<td>12</td>
<td>&lt;0.001</td>
<td>0.84</td>
</tr>
<tr>
<td>Period $\times$ Group</td>
<td>0.34</td>
<td>1</td>
<td>12</td>
<td>0.571</td>
<td>0.03</td>
</tr>
<tr>
<td>Force</td>
<td>62.60</td>
<td>1</td>
<td>12</td>
<td>&lt;0.001</td>
<td>0.84</td>
</tr>
<tr>
<td>Force $\times$ Group</td>
<td>0.40</td>
<td>1</td>
<td>12</td>
<td>0.540</td>
<td>0.03</td>
</tr>
<tr>
<td>Period $\times$ Force</td>
<td>4.81</td>
<td>1</td>
<td>12</td>
<td>0.049</td>
<td>0.29</td>
</tr>
<tr>
<td>Period $\times$ Force $\times$ Group</td>
<td>1.41</td>
<td>1</td>
<td>12</td>
<td>0.258</td>
<td>0.10</td>
</tr>
<tr>
<td>Group</td>
<td>11.48</td>
<td>1</td>
<td>12</td>
<td>0.005</td>
<td>0.49</td>
</tr>
</tbody>
</table>

Note: The significant $P$ values are in bold.
higher level of alpha SP may be associated with higher attentional involvement in the task and more efficient sensorimotor integration as suggested by our previous study (Kristeva et al. 2007).

Several authors suggested the coherence itself as a mechanism for effective communication because "it renders mutual input optimally timed and therefore maximally effective" (Schoffelen et al. 2005) (cf. also Fries et al. 2007; Kristeva et al. 2007; Womelsdorf et al. 2007; Engel and Fries 2010; Hipp et al. 2011; Singer 2011). Phase synchronization supports both working and long-term memory and acts by facilitating neural communication and by promoting neural plasticity, that is, neural communication and plasticity may support each other (Buzsaki 2006; Fell and Axmacher 2011). In our study, the communication between motor cortex and alpha-motoneurons probably induces synaptic plasticity between both networks. On the other hand, the strengthened synaptic connections between these 2 regions during motor adaptation may more easily induce the phase synchronization and therefore the higher CMC (Fell and Axmacher 2011).

But the CMC is not an "efferent phenomenon" only. Several studies showed the role of the afferent feedback and of the sensorimotor integration in the generation of the CMC (Fetz et al. 2002; Fisher et al. 2002; Baker et al. 2006; Patino et al. 2008). One can speculate that motor adaptation improves the sensorimotor integration and therefore the cortical motor synchrony that drives stronger the motoneuronal pool as reflected in the higher CMC. We suggest the following underlying physiological mechanism: the performance of the motor task by the finger is perceived not only by the muscle spindles but also by the skin and joints receptors and by the secondary endings. All those structures contribute to the facilitatory input to the fusimotor system, which in turn could affect the sensitivity of the muscle spindles. The increased tactile and muscle spindles sensitivity during motor adaptation can enhance the sensorimotor integration at cortical level and therefore the cortical motor synchrony (Nelson et al. 1980).

Differences in the sensitivity threshold to the used force could explain the observation that some individuals initially demonstrate CMC, whereas others do not. This implies that a response to the particular force level would develop with learning, respectively, motor adaptation.

**Two Different Groups in Terms of Oscillatory Motor Control on the Basis of CMC**

During SF, Group CMC++ (8/14 subjects) presented beta-range CMC at the beginning of the experiment and Group CMC++ (6/14 subjects) presented such after learning. The proportion of subjects presenting significant beta-range CMC is in line with James et al. (2008), Mima et al. (2000), Baker MR and Baker SN (2003), Hashimoto et al. (2010) and our previous experience. Both groups had the same behavior during DF control: Again Group CMC++ presented CMC after learning only.

The cortical activation as quantified by the TRD (Pfurtscheller 1977; Pfurtscheller and Lopes da Silva 1999) was stronger for Group CMC++ than for Group CMC++ (Fig. 6 and Table 3). That Group CMC++ is more desynchronized during the task can be seen also from the lower cortical motor alpha, beta, and gamma SP in comparison to the SP of Group CMC++ (Figs 4 and 5). Figures 4 and 5 also demonstrate that for both Groups learning is associated with higher SP, that is, with higher cortical motor synchrony.

The Group which presented CMC from the very beginning had generally better performance than the other group (see Fig. 4C,F and Fig. 5C,F). Furthermore, during the more difficult DF, this group showed greater improvement suggesting faster learning of the task. This suggests that only those subjects presenting a better corticomuscular tuning are able to improve quickly on motor tasks of the nature used in this study.

Although having worse performance, the Group that presented CMC only after learning was more desynchronized during both SF and DF (see Fig. 4C,F and Fig. 5C,F). This was the case before and after learning. Therefore, we suggest that Group CMC-> has lower cortical motor efficiency because for the same performance it needs stronger cortical activation.

**Cortical Activation during SF and DF**

DF control was associated with stronger cortical activation than static one as quantified by the stronger TRD (Fig. 6). Furthermore, the state of the cortical motor network was characterized with significant beta-range SP decrease, a finding which is in line with previous results of ours (Omlor et al. 2007). This is also in line with Spinks et al. (2008) who found that the majority of M1 neurons showed higher beta-range LFPs power during simple grips, whereas complex grips like precision grip were associated with small beta power.

**CMC during Isometric Compensation for Low-Level Isometric Forces at 8% MVC**

Here, we show that DFs at 8% MVC are accompanied with a reduction of the beta-range CMC and shift toward higher gamma-subrange frequencies (30--45 Hz) (Figs 2 and 3). This means that the behavior of the corticospinal network at 8% MVC is the same as shown by us for 4% MVC (Omlor et al. 2007).

At first sight, this seems at odds with our previous findings reported in Chakarov et al. (2009) showing that isometric compensation for modulated forces at 8% MVC is related to broad beta-range CMC. However, one has to take into consideration that modulated forces at 8% MVC in Chakarov et al. (2009) were presented in the context of a task with increasing modulated forces (from 8% MVC to 16% MVC and 24% MVC). Brain states are context dependent (Buzsaki 2006, p. 262--276) and therefore it is not surprising that in the Chakarov's study beta-range CMC subserves modulated forces and in our task static ones. This context-dependency of CMC show that similar to the cognitive systems, there is no one-to-one relationship between frequency band and function in the motor system (Tallon-Baudry 2009). The exceptional S7 from this study presenting not gamma but low-amplitude beta-range CMC during modulated force provides another argument for this statement (Figs 2 and 3).

In sum, the present investigation documents for the first time an explicit description of the occurrence of CMC in all experimental subjects investigated and the possible role of individual differences in the occurrence of CMC that can be changed with learning. Furthermore, we show that increased cortical motor and corticospinal synchrony are related to better performance. Further studies have to be designed to increase the cortical motor synchrony in order to improve the performance. These results could have important implications for the use of cortical oscillatory activity in BCI applications.
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References


