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Gamma-range corticomuscular coherence during dynamic force output

Wolfgang Omlor,[a] Luis Patino,[a] Marie-Claude Hepp-Reymond,[b] and Rumyana Kristeva[a,*]

[a]*Neurological Clinic, Albert-Ludwigs-University, Breisacher Straße 64, 79106 Freiburg, Germany*
[b]*Institute of Neuroinformatics, University and ETH, Zürich, Switzerland*

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The beta-range synchronization between cortical motor and muscular activity as revealed by EEG/MEG–EMG coherence has been extensively investigated for steady-state motor output. However, there is a lack of information on the modulation of the corticomuscular coherence in conjunction with dynamic force output. We addressed this question comparing the EEG–EMG coherence and the cortical motor spectral power in eight healthy subjects in a visuomotor task, in which the subjects exerted a steady-state or periodically modulated dynamic isometric force output with their right-index finger to keep a visual cursor within a target zone. In the static condition, significant coherence was confined to the beta-range. In the dynamic condition, the most distinct coherence occurred in the gamma-range and the significant beta-range coherence was strikingly reduced. The cortical motor power in the beta-range during dynamic force output was decreased, whereas the power in the gamma-range remained without significant change. We conclude that during dynamic force the corticospinal oscillation mode of the sensorimotor system shifts towards higher (principally gamma) frequencies for the rapid integration of the visual and somatosensory information required to produce the appropriate motor command.

Keywords: EEG; Beta band; Gamma band; Coherence; Spectral power; Force; Precision grip

Introduction

Synchronized oscillatory activity of cortical neurons is a well-known phenomenon in the cerebral cortex. In visual areas, phase-locked oscillations of spatially separated neuronal assemblies at approximately 40 Hz are supposed to subserve binding of disparate visual features into a coherent percept (Singer and Gray, 1995). With respect to the motor system, previous studies demonstrated the presence of oscillatory local field potentials in the beta-range (at 20–30 Hz) in the sensorimotor cortex of monkeys during different voluntary movements such as reaching and grasping (Murthy and Fetz, 1992, 1996; Donoghue et al., 1998). Such beta-range oscillations can influence descending motor commands to the contralateral hand muscles, giving rise to constant phase relations between cortical and electromyographic oscillations as assessed by the coherence function (Baker et al., 1997). Similarly, beta-band coherence between contralateral motor cortex and hand muscles has been observed in humans during maintained contraction using MEG (Conway et al., 1995; Baker et al., 1997, 1999; Salenius et al., 1997; Brown et al., 1998; Kilner et al., 2000) and surface EEG (Halliday et al., 1998; Mima et al., 2000; Kristeva-Feige et al., 2002). Both in humans and monkeys, beta-band corticomuscular coherence (CMC) showed a clear task dependence, occurring most distinctly during immutable states of motor output while being abolished during the phasic part of the movement (Baker et al., 1997; Kilner et al., 1999; Feige et al., 2000). Phase coherence calculations between cortical oscillations and hand muscle activity in the beta-range provide support for the hypothesis that fast pyramidal pathways are involved in the mediation of this coherence (Gross et al., 2000). The presence of synchronous descending commands may yield a more efficient recruitment of motor units and thereby reflect a mechanism of efficient corticospinal interaction (Kristeva et al., submitted for publication; Baker et al., 1997; Salenius et al., 1997).

Despite extensive investigation of synchronization between cortex and muscle activity during steady-state motor output (static force or precision grip), there is still a lack of information on the modulation of CMC in conjunction with dynamic force. The present study addressed this question by comparing the EEG–EMG coherence during a static and dynamic condition which differed from each other only in the force pattern.

Marsden et al. (2000) compared ECoG/EMG coherences in humans during self-paced maximal tonic contractions and self-paced phasic movements of the upper limb muscles. They found a tendency for a task dependency as coherences above 30 Hz tended

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* Corresponding author. Fax: +49 761 270 5416.
E-mail address: kristeva@nz.ukl.uni-freiburg.de (R. Kristeva).
URL: http://www.uniklinik-freiburg.de/neurologie/live/forschung/xpeeg.html (R. Kristeva).

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to occur more often during the phasic movements. Based on the results of Marsden et al. (2000), we hypothesized that dynamic isometric force output may require a more complex sensorimotor processing and thus would be also accompanied by corticospinal oscillations at gamma frequencies. We clearly show that, in the static force condition, significant coherence was confined to the beta-range and that in the dynamic force condition the most distinct coherence was shifted to a high beta- or low gamma-range.

Methods

Subjects

Eight healthy subjects (mean age 29 ± 13 years, 4 men) without any history of neurological disease participated in the study. All subjects were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). They gave written consent prior to the experiment in accordance with the declaration of Helsinki, and all procedures were approved by the local ethics committee. Any 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.* Figs. 1a, b).

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 (TF). The subject had to compensate the force generated by the manipulandum isometrically and maintain the ring in its initial position. The force exerted by the subject was called exerted force (EF). Visual feedback about the position of the ring was provided to the subject via a monitor 60 cm in front of him/her with two circles (Fig. 1c). The green outer circle was fixed 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 then to apply the same force in the opposite direction (here flexion) to keep the ring in its central position. The sensitivity of the visual feedback with respect to the finger position was 2.85 mm for 1 mm.

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

- *Static force output condition*: during this condition, the manipulandum generated a steady force at 4% of the maximum voluntary contraction (MVC) determined prior to the experiment (Fig. 1d).
- *Dynamic force output condition*: during this condition, the manipulandum generated a sinusoidal modulation of the 4% MVC force at a frequency of 0.7 Hz and with peak-to-peak amplitude of 1.6% MVC (Fig. 1e).

The mean force was the same for both conditions. We used such low force because it has been shown that the motor cortical neurons are most sensitive within a low force range (Hepp-Reymond et al., 1989). In both cases, the generated force had to be compensated isometrically. 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 to 4% MVC, the subject had to

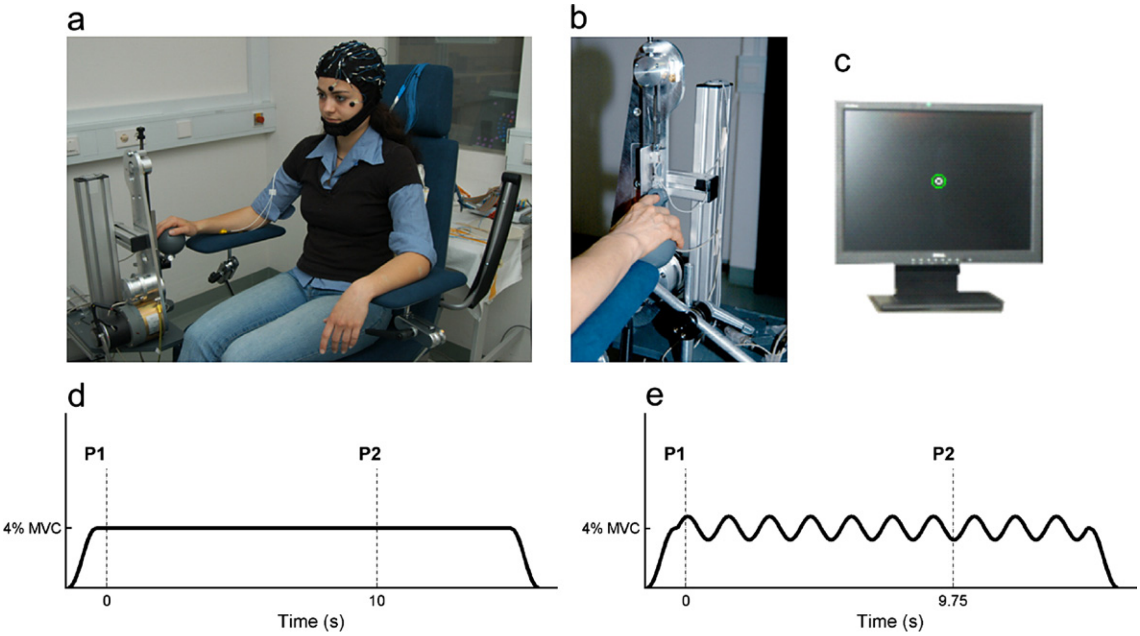

Fig. 1. (a) High-resolution EEG recorded from 52 scalp positions together with the electrooculogram (EOG) and the EMG. (b) Manipulandum. (c) Visual feedback about the position of the ring displayed on a monitor in front of the subject. (d) Force profile generated by the manipulandum during static and (e) dynamic condition. After a gradual increase of force to 4% MVC, the subject has to maintain the ring in its central position for 15 s. The dynamic condition has a superimposed sinusoidal function.

maintain this force level with the ring in its central position for approximately 15 s. The task included a series of 35 trials of 15 s each. Rest intervals of 5 to 10 s were included between the trials. The subjects were instructed to avoid any other movements and to fix their gaze on the visual feedback during the task.

Recordings

Electrical potentials (bandpass 0–200 Hz, sampling rate 1000 Hz) were recorded from 52 scalp positions according to the international 10–20 system (Synamp 2, NeuroScan, El Paso, TX, USA) referenced to Cz (Fig. 1a) with ground at FzA. Electrode impedances were under 5 kΩ. The electrooculogram (EOG, same bandpass and sampling rate as for EEG) was recorded to exclude trials contaminated with eye movements from further analysis. Electromyographic activity (EMG, bandpass 5–200 Hz; sampling rate 1000 Hz) was recorded from the pars indicis of the right flexor digitorum superficialis muscle, the prime mover of the index finger flexion.

The set-point of the force in the manipulandum (TF), together with the exerted force of the subject (EF), was recorded in parallel with the electrophysiological data (same bandpass and sampling rate as for EEG). EEG, EOG and EMG were stored and analyzed off-line.

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 phase were not dealt with in this study. Continuous data, in-between manually put markers (P1 and P2), were further divided into successive segments of 512 ms length, allowing for a frequency resolution of 1.96 Hz (Figs. 1d, e). The EEG signal was then transformed into the reference-free current source density distribution (CSD) which reflects the underlying cortical activity and removes nearly all volume conduction effects (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 1.05" (MES, Münich, Germany). A total of 300 artifact-free segments were analyzed for each subject.

EMG signal was rectified as it is known that full wave rectification provides the temporal pattern of grouped firing motor units (Halliday et al., 1995). 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

$$\mathrm{SP}_c(f) = \frac{1}{n}\sum_{i=1}^{n} C_i(f)C_i^*(f)$$

where C_i represents the Fourier transformed channel c for a given segment number (i=1….n) and '*' indicates the complex conjugate.

Coherence values (Coh) were calculated between the rectified EMG and the EEG channels in order to calculate the synchronization between the two signals. Coherence values (Coh) were calculated on the basis of the following formulae:

$$\mathrm{Coh}_{\mathrm{c1,c2}}(f) = \frac{|S_{\mathrm{c1,c2}}(f)|^2}{|\mathrm{SP}_{\mathrm{c1}}(f)| \times |\mathrm{SP}_{\mathrm{c2}}(f)|}$$

where

$$S_{\mathrm{c1,c2}}(f) = \frac{1}{n}\sum_{i=1}^{n} \mathrm{C1}_i(f)\mathrm{C2}_i^*(f)$$

thus $S(\mathrm{c}_1,\ \mathrm{c}_2)$ (f) is the cross-spectrum for the EEG signal in channel c1 and the rectified EMG signal in channel c2 at a given frequency f and $\mathrm{SPc}_1(f)$ and $\mathrm{SPc}_2(f)$ are the respective power spectra for c1 and c2 at the same frequency. For frequency f, the coherence value, $\mathrm{Coh}(\mathrm{c}_1,\ \mathrm{c}_2)$ (f), thus corresponds to the squared magnitude of a complex correlation coefficient. $\mathrm{Coh}(\mathrm{c}_1,\ \mathrm{c}_2)$ (f) is then a real number between 0 and 1.

Coherence is considered to be significant if the resulting value lies above the confidence level (CL) (Rosenberg et al., 1989)

$$\mathrm{CL}(\alpha) = 1 - (1-\alpha)^{\frac{1}{n-1}}$$

where n is the number of segments and alpha, 'α', is the desired level of confidence. We considered coherence to be significant above the 95% confidence limit.

The highest coherence peaks were over the left motor cortex contralateral to the active right index finger (EEG channels C1 and C3). For the grand average, we have always chosen the channel with the highest coherence (C1 or C3).

Statistical analysis of the spectral power and coherence

To test for any statistical difference on CMC and cortical power between the static and dynamic condition, we measured the area under the coherence curve and above the significance level, A_{coh}, and under the spectral power curve, A_{pow}, in-between two frequency windows: 15–30 Hz for beta then 30–45 Hz for gamma-range.

Individual values for the area of the coherence were firstly transformed logarithmically to yield symmetric distributions according to the formula

$$A'_{\mathrm{coh}} = \log(0.0001 + A_{\mathrm{Coh}})$$

To evaluate the relation in magnitude between beta- and gamma-range coherence, we subtracted to the coherent area in beta-range the significant area corresponding to the gamma-range.

$$A = A'_{\mathrm{Coh(beta)}} - A'_{\mathrm{Coh(gamma)}}$$

We then performed a non-parametric test on the resulting values A for CMC, and A_{pow} for spectral power, the paired Wilcoxon test of the null hypothesis that the difference between the matched samples of coherence and power spectra from static and dynamic conditions comes from a distribution which is symmetric around zero.

We used a third window between 15 and 45 Hz to evaluate the whole beta- and gamma-range activity together and calculated its center of gravity. We then applied the paired Wilcoxon test on the frequency values obtained from the center of gravity for the static and the dynamic condition to look for any significant frequency shift.

Results

Corticomuscular coherence (CMC)

The main difference between both conditions was that dynamic force output was accompanied by an increased CMC in the gamma-range and the static one by a broad-band beta-range CMC. The shift of the main coherence to higher frequencies during dynamic force output was not related to any alteration of the topographic distribution of the maximum coherence.

Fig. 2 shows original curves of CMC for both static (left column) and dynamic (right column) conditions of two representative subjects (subjects 1 and 2).

Subject 1 presents during the static force condition beta-range CMC; significant coherence occurs, but only to a lower degree, also in the low gamma-range. In the dynamic force condition, the CMC occurs in gamma-range and the beta-range CMC is almost completely abolished. We found this pattern of activation in six out of the eight subjects studied.

The two remaining subjects presented another pattern of CMC, namely, for both static and dynamic force conditions the most prominent coherent activity appears predominantly in the beta-range. Subject 2 shown in Fig. 2 is one of these two subjects with this pattern. Nevertheless, it must be observed that the beta-range CMC during the dynamic condition is reduced compared to the CMC in the static condition. The gamma-range CMC in the dynamic condition is enhanced, but only to a lower degree as compared to subject 1.

When the results are pooled for all subjects, the following picture occurs (*cf.* grand average in Fig. 2): during static force, there is a significant broad-band beta CMC with two predominant peaks at 17.6 Hz and 23.4 Hz. Across subjects, the maximum amplitude of the beta-range CMC ranged from 0.013 to 0.124. Although significant coherence occurs to a lower degree in the low gamma-range, the beta-range coherence outgrows systematically the gamma-range CMC. In the dynamic condition, the most prominent CMC occurs in the gamma-range, with a peak at 37.1 Hz. The CMC in the dynamic force condition yielded maximum values from 0.012 to 0.105. Overall, the beta-range CMC was considerably diminished compared to that in the static force condition (*cf.* Fig. 2), however there existed still some coherent activity in the beta-range. Two small peaks at 19.5 Hz and at 27.3 Hz remained over the confidence level, most probably representing the influence of subjects 2 and 4 (who also had high beta-range CMC in the dynamic condition). Apart from these subjects, we found that the gamma CMC was constantly higher than that in the beta-range. However, when we compare the dynamic condition with the static one, the beta CMC for all subjects decreased strongly while the gamma CMC increased. Indeed, the change in the relation beta-gamma coherence (given by the difference between beta and gamma CMC) from the static to the dynamic condition is statistically significant ($p = 0.0078$, Wilcoxon paired test, $n = 8$).

To visualize the shift of the frequency of the CMC towards higher frequencies from static to dynamic force, we calculated the

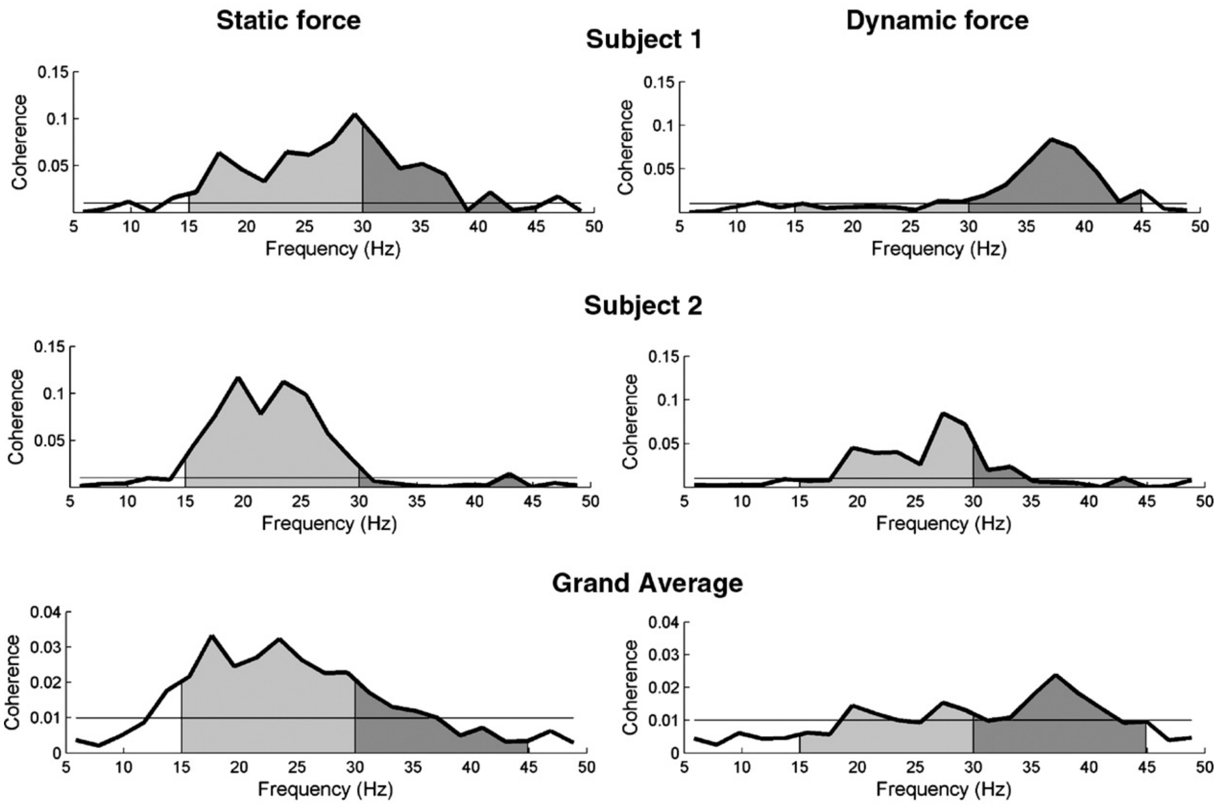

Fig. 2. Frequency-coherence plots for EEG–EMG coherence during static force (left panel) and during dynamic force (right panel) for subjects 1 and 2, and for all 8 subjects (Grand average). The beta-range (15–30 Hz) is marked in light gray, the gamma-range (30–45 Hz) in dark gray. Note that during the static condition the most prominent activity occurs in the beta-range. During the dynamic condition, previous beta-range coherence is decreased and the general activity is shifted towards high frequencies, principally in gamma-range.

center of gravity for the significant coherent area over the frequency range of 15–45 Hz in each individual coherence spectrum. Indeed, in every subject, the center of gravity of the coherent activation from static to dynamic condition is shifted to higher frequencies as can be observed in Fig. 3. The extent of the shift varies between 5 and 18 Hz. This shift to higher frequencies was statistically significant ($p=0.0078$, Wilcoxon test $n=8$). In four of the subjects (1, 3, 7 and 8), the center of gravity was shifted from beta- to gamma-range indicating that the coherent activity in those frequency bands was very contrasting between the static and dynamic condition. In two of the subjects (5 and 6), the shift occurred within the gamma-range mostly because the CMC in the static condition was in the high beta band together with some coherence in low gamma band. For subjects 2 and 4, for which we previously mentioned that their maximum of coherence occurred in the beta band during both conditions, a shift of coherent activity towards higher frequencies is also observed but the CMC remains in high beta-range. Overall, the shift of the combined beta and gamma activity towards higher frequencies that occurs in all subjects confirms that the dynamic force output is characterized by a decrease of beta-range combined with an increase of gamma CMC. Interestingly, the shift of the frequency of the CMC was rather constant from subject to subject (with subject 8 as the only exception; SD 2.9 Hz without this subject), whereas the inter-individual differences in coherence frequency were much larger: the center of gravity for subjects 1–7 had a SD 3.94 Hz during static and 5.54 Hz during dynamic force output.

Cortical motor spectral power (SP)

The cortical motor power was as well modulated by both conditions.

Fig. 4 presents original curves of the cortical motor SP for static and dynamic conditions for the same two representative subjects as in Fig. 2. For subject 1, beta-range synchronization was only present during the static force output. For subject 2, an important amplitude decrease of the beta-range cortical SP was observed in the dynamic force condition, although a small peak still remained.

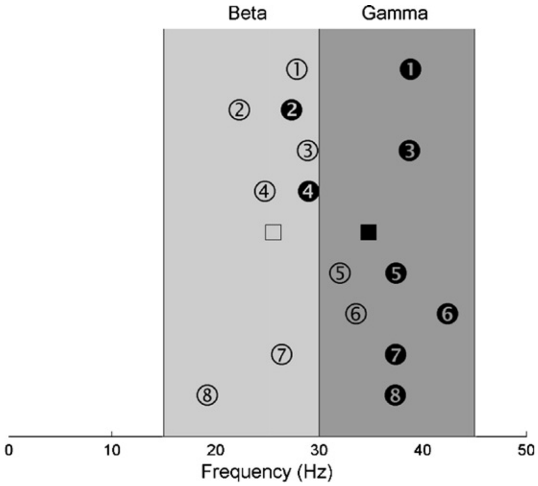

Fig. 3. (a) Individual frequency values of maximum coherence (center of gravity) calculated for the beta-range (15–30 Hz) and for the gamma-range (30–45 Hz). Each subject is represented with a number. Empty circles and square: individual values and their mean for the static condition. Filled circles and square: values and mean for the dynamic condition. The beta-range is marked in light gray, the gamma-range in dark gray. Note that the frequency values for the dynamic condition are systematically higher than for the static condition.

The SP grand average for the eight subjects disclosed that during the static condition the beta SP was clearly stronger than the gamma SP but that it was radically diminished in the dynamic force condition ($p=0.0078$, Wilcoxon test $n=8$). The gamma SP was increased in the dynamic force condition in six out of the eight subjects investigated, but this effect was not significant (*cf.* Fig. 4).

Discussion

Previous studies have shown that static force output is accompanied by beta-range corticomuscular coherence (Conway et al., 1995; Baker et al., 1997, 1999; Salenius et al., 1997; Brown et al., 1998; Halliday et al., 1998; Feige et al., 2000; Mima et al., 2000; Kilner et al., 2000). In accordance with these results, we found a significant broad-band beta-range CMC during the static force output. However, the present results extend our knowledge of corticospinal interactions during isometric motor tasks with regard to the following novel aspect: The isometric compensation of dynamic force modulations is accompanied by a shift of CMC to higher (principally gamma) frequencies while the CMC in the low beta band is strikingly reduced. Corticomuscular gamma-band coherence had been observed so far only during maximum voluntary contraction and during slow movements (Brown et al., 1998) or during phasic movements (Marsden et al., 2000).

It is worth mentioning that we have not exclusively found gamma CMC during the dynamic force output: The coherence focus of two subjects (S2 and S4) does not exceed the gamma threshold but occurs at high beta frequencies. Nevertheless, for these two subjects, there is also a decrease of beta-band coherence concomitant with an increase of the gamma-band coherence when static and dynamic conditions are compared. Overall, the shift of the coherence to higher frequencies (gamma or in two subjects high beta) during dynamic force as compared to the static force condition is consistent in all subjects. Therefore, it seems to be reasonable to assume a related underlying mechanism concerning the coherence at high beta and in the majority of subjects at low gamma-range. The sensorimotor system obviously resonates at higher frequencies when dynamic instead of static force is required.

CMC also mirrors synchrony of separated cortical neuronal ensembles with one another (Marsden et al., 2000). Gamma-band oscillations in particular are thought to provide a mechanism for the binding together of functionally related cortical elements such as in visual attention (Fries et al., 2001), motor planning (Brown and Marsden, 1998; Donoghue et al., 1998), sensory (Meador et al., 2002; Bauer et al., 2006), sensorimotor as well as visuomotor integration (Aoki et al., 1999, 2001) and cognition (Tallon-Baudry and Bertrand, 1999). Compared to the static force, the exact isometric tracking of the periodically modulated force in our study requires the allotment of higher attention resources and a more complex and continuous dynamic integration of visual as well as somatosensory information. In this regard, the shift of the main coherence to higher frequencies might reflect binding together of the complex tactile, proprioceptive and visual information into an appropriate motor program and its effective transmission to the subsequent spinal motoneurons.

Neuronal populations which are coherent with their target group provide maximally effective input, as a result of their precise

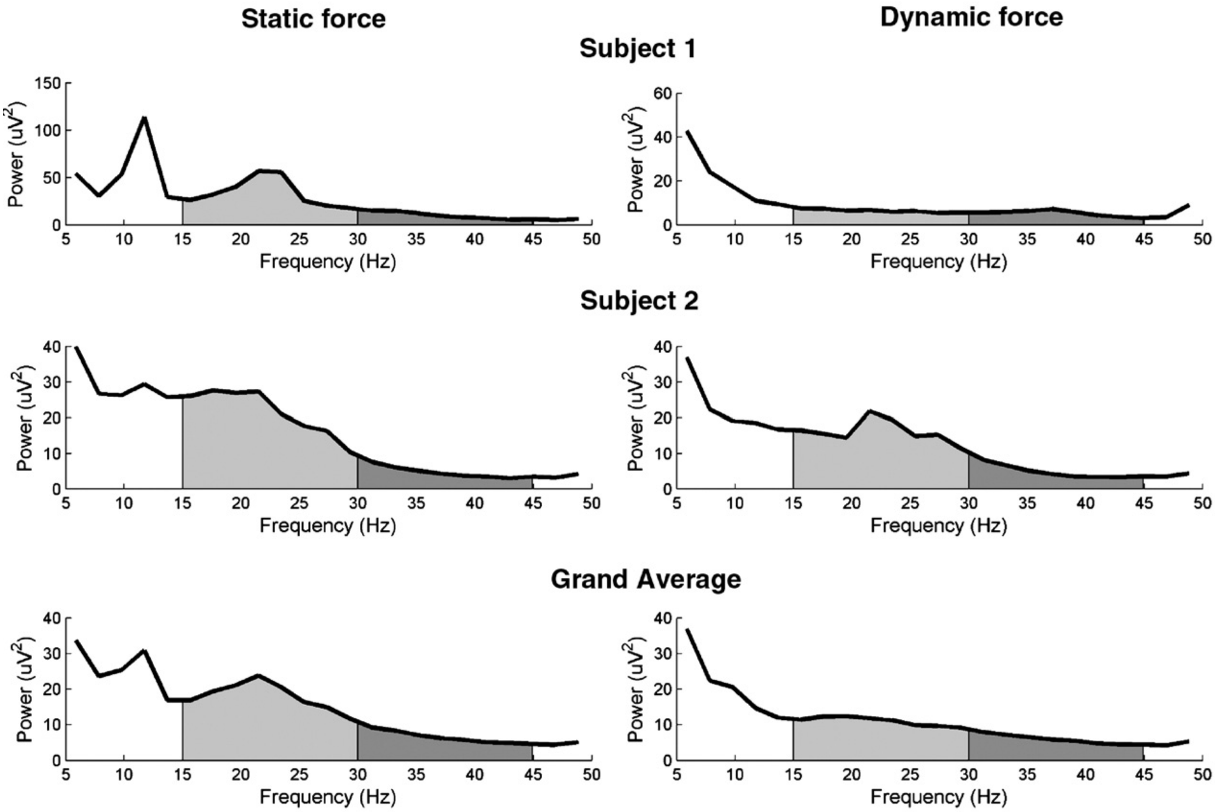

Fig. 4. EEG spectral power during static force output (left panel) and during dynamic force output (right panel) for subjects 1 and 2, and for all 8 subjects (grand average). The beta-range (15–30 Hz) is marked in light gray. The gamma-range (30–45 Hz) is marked in dark gray. Note that the beta-range cortical power is reduced in the dynamic condition.

timing with the excitability peaks of the target neurons (Volgushev et al., 1998). At gamma frequencies, each cortical or spinal neuron features more excitability peaks per time unit than it would have when resonating at beta frequencies. Thus, the potential of coherent corticospinal networks to integrate task-relevant somatosensory and visual information is much higher when they are coherent at higher frequencies since one separate neuron could fire at various combinations of the excitability peaks of cortical or spinal neurons to convey its information to the target network. Thus, the oscillation of corticospinal networks at higher frequencies might facilitate the rapid recalibration of the sensorimotor system demanded by the dynamic force condition of our study.

Schoffelen et al. (2005) found that readiness to respond with a phasic motor action induces gamma CMC during reaction time tasks. Our study shows the existence of gamma CMC during isometric compensation of a periodically modulated force whereby joint movements are absent or negligible. These results are related to the findings of Schoffelen et al. (2005) with regard to one important aspect: readiness to respond also arises in our dynamic force condition as a consequence of its periodic and thereby predictable temporal structure, permitting subjects to react in anticipation to the sinusoidal force modulations. Prediction and anticipation are closely related and may entail readiness to respond and motor planning with concomitantly higher levels of attention.

The role of CMC in bringing effectively together selected cortical elements into the motor act has been suggested by Marsden et al. (2000): coherence tends to shift to new frequencies when different tasks are performed, despite the involvement of the same muscles. Additionally, coherence above 30 Hz tended to occur more frequently during phasic movements than during maximal tonic contractions. However, it cannot be deduced from the results of Marsden et al. (2000) to what extent changes in limb displacement and differences in force level gave rise to the different frequencies in their results. In contrast, in our study, we clearly show that the significant shift of the CMC frequency towards higher frequencies is related to the different force conditions. To note, Macefield et al. (1996) suggested that particularly tactile afferents are capable of triggering an appropriate change of the exerted force in response to an imposed change in load force. Thus, we show that oscillation of corticospinal networks at higher frequencies might facilitate the rapid integration of tactile, proprioceptive, visual and cognitive (prediction and planning) information during isometric compensation of a dynamic force.

In steady-state force tasks, beta CMC coincides with cortical motor beta-band power and thereby decreased cortical excitability. This is supposed to suppress other cortical activities during states of immutable force output (Kristeva et al., submitted for publication; Brown, 2000). If so, it is not unexpected that beta CMC is related to concomitant beta-band SP. The beta CMC decrease in the dynamic condition was accompanied by a beta SP decrease. In contrast, the gamma SP was not significantly affected during the dynamic condition although an increase of the gamma SP was observed in 6 out of the 8 subjects. This suggests that gamma-band CMC is related to gamma-band SP to a lower degree than beta CMC to beta SP. These findings are supported by similar results related to dependency of CMC on SP at beta and gamma frequencies: Schoffelen et al. (2005) showed that an increase of the gamma-range coherence during shorter reaction times is not dependent on the increase of the gamma spectral power. Moreover, in their task, there were periods with steady-state motor output characterized with beta-range CMC that was not fully independent of the beta spectral power. In another study, we also found that the magnitude of the beta CMC is not completely independent from the magnitude of beta-range cortical motor SP (Kristeva et al., submitted for publication).

To conclude, the presence of a rhythmic beta drive to muscles may be largely constricted to stable, immutable states in motor output with low computational load and thereby reflects an efficient mechanism for motor unit recruitment during steady-state contractions (Baker et al., 1997; Brown, 2000). On the other hand, we observed CMC at higher frequencies during a more complex, but predictable task with a periodic design. We suggest that corticomuscular coherence at higher frequencies (gamma or high beta) is predominantly engaged in dynamic and predictable force output as a mechanism for binding visual and particularly cognitive as well as somatosensory feedback information to ensure an appropriate motor response. All these findings have implications for the role of the corticomuscular coherence in fine and precise motor control.

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