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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

* 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

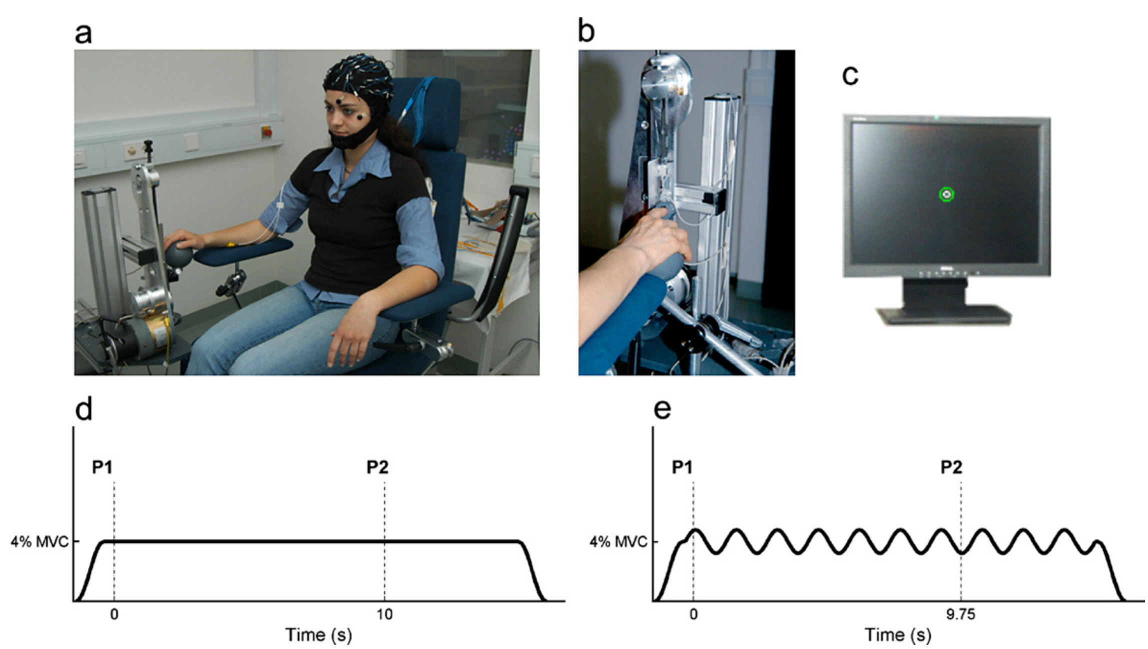

Fig. 1. (a) High-resolution EEG recorded from 52 scalp positions together with the electrooculogram (EOG) and the EMG. (b) Manipulandum. (c) Visual feedback about the position of the ring displayed on a monitor in front of the subject. (d) Force profile generated by the manipulandum during static and (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.