Absence of Gamma-Range Corticomuscular Coherence During Dynamic Force in a Deafferented Patient

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INTRODUCTION

It is believed that synchronization between motor units during isometric contraction and force generation can be attributed to the synchronization of motor cortical neurons projecting to the spinal cord. Previous studies have shown the presence of oscillatory local field potentials at 20–30 Hz in the sensorimotor cortex of monkeys during various wrist and digit movements (Murthy and Fetz 1992, 1996; Sanes and Donoghue 1993). In humans, beta-range synchronization, as assessed by the coherence function, has been found between the contralateral motor cortex and electromyographic oscillations of hand muscles during static (steady-state) motor output (Baker et al. 1997; Conway et al. 1995; Feige et al. 2000; Gross et al. 2000; Halliday et al. 2000; Kilner et al. 1999; Kristeva et al. 2007; Kristeva-Feige et al. 2002; Mima and Hallett 1999; Salenius et al. 1997). Although the general view is that corticomuscular coherence (CMC) is generated in efferent motor networks (Farmer et al. 1993), recent studies brought some evidence thatafferent feedback plays a role in the beta-range CMC. This was shown by modulating peripheral feedback with transient deafferentation, such as digital nerve anesthesia (Fisher et al. 2002), ischemia-induced deafferentation (Pohja and Salenius 2003), or by the manipulation of nervous conduction with cooling (Riddle and Baker 2005). Based on the fact that afferent fibers can fire in partial synchrony with oscillations in cortex and muscles, Baker et al. (2006) also suggest that both ascending and descending pathways may mediate coherence.

Recently, we studied CMC in a visuomotor task in which the subjects had to isometrically compensate a dynamic periodically modulated force applied on their right index finger (Omlor et al. 2007). In contrast to the well-documented broadband beta-range CMC obtained during static force, we observed that, during the isometric compensation of the periodically modulated force, the most distinct CMC occurred in the gamma-range. We concluded that during dynamic force the sensorimotor system resorts to a new oscillation mode and resonates at gamma-range frequencies to rapidly integrate the visual and proprioceptive information needed to produce the appropriate motor command.

In this study, we tested the role of the proprioceptive afferent feedback in the generation of gamma-band CMC during isometric compensation of dynamic forces by investigating the deafferented patient GL and six age- and sex-matched subjects performing the same motor task as in Omlor et al. (2007). Our results indicate that the generation of gamma-band CMC requires proprioceptive information.

METHODS

Subjects

The deafferented patient GL, a right-handed 56-year-old woman, participated in the study (for detailed clinical description, see Forget and Lamarre 1987 and http://deafferented.apinc.org). In brief, after two episodes of polyneuropathy (at the age of 27 and 31 yr), the patient has been suffering from a strong sensory impairment of the whole body up to below the nose because of affected large diameter peripheral sensory myelinated fibers. The impairment was documented by sural biopsy. The patient has a total loss of touch, vibration, pressure, and kinesthetic senses and no tendon reflexes in the four limbs. Pain and temperature sensations are still present. The motor fibers are not affected, and the patient can perform complex motor tasks under visual guidance. The patient GL is the model of choice for this study because she has previously helped to clarify the role of sensory information in weight discrimination (Fleury et al. 1995), simple limb movements (Hepp-Reymond et al. 2001), response monitoring (Allain et al. 2004), EMG oscillatory activity (Kilner et al. 2004), the voluntary movement organization (Kristeva et al. 2006), and the oscillatory cortical activity during isometric contraction (Patino et al.)
Six healthy right-handed female subjects (mean age, 50 ± 5 yr) without any history of neurological disease participated in the study as age- and sex-matched controls. The handedness of patient and controls was tested according to the Oldfield questionnaire (Oldfield 1971).

All subjects participated according to the Declaration of Helsinki, with informed consent and the approval of the local ethics committee.

**Paradigm**

During the experimental session, the subject sat in an electrically shielded, dimly lit room. The right arm was supported in 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 (Fig. 1, A and 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 upward forces on the ring. The subject had to compensate this force, called target force (TF), to maintain the ring in its initial position. The quasi-isometric flexion 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 19-in monitor placed 90 cm in front of her with two circles at the level of the eyes (Fig. 1C). The green outer circle was fixed and represented the ring’s reference position, whereas 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 then 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 corresponded to 2.85 mm on the screen for 1-mm ring displacement. During the experiment, the finger and ring were hidden from the field of view of the subject by a piece of cardboard.

Two different experimental conditions were studied in a given recording session: 1) static force condition, the manipulandum generated a steady force at 4% of the maximum voluntary contraction (MVC) determined before the experiment (Fig. 1D); 2) dynamic force condition, the manipulandum generated a sinusoidal modulation of the 4% MVC force at frequency of 0.7 Hz and with peak-to-peak amplitude of 1.6% MVC (Fig. 1E).

The mean force was thus 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). 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 maintain this force for ~15 s. The task included a series of 35 trials of 15 s each. Rest intervals of 5–10 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. The subjects were given some practice to become sufficiently familiar with the task.

**Recordings**

Electrical potentials (EEG; band pass, 0–200 Hz; sampling rate, 1,000 Hz) were recorded from 52 scalp positions according to the international 10–20 system (Synamp 2, NeuroScan, El Paso, TX) referenced to Cz (Fig. 1A) with ground at FzA. Electrode impedances were kept <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. EMG activity
(band pass, 5–200 Hz; sampling rate, 1,000 Hz) was recorded from the pars indicis of the right flexor digitorum superficialis muscle, the prime mover of the index finger flexion with surface electrodes, and from the first dorsal interosseus muscle. For the EMG recordings, belly-tendon montage was used with the active electrode placed over the muscle belly.

The force generated by the manipulandum (TF) and the force exerted by the subject (EF) were recorded in parallel with the electrophysiological data (same band-pass 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 were not dealt with in this study. Continuous data, in between manually placed markers P1 and P2 (Fig. 1, D and E), were further divided into successive segments of 512-ms length, allowing for a frequency resolution of 1.96 Hz. The EEG signal was transformed into the reference-free current source density distribution (CSD), which 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 BrainVision 1.05 (München, Germany). A total of 300 artifact-free segments were analyzed for each subject.

The EMG signal was rectified because it is known that full wave rectification provides the temporal pattern of grouped firing motor units (Halliday et al. 1995). The discrete 512-point Fourier transform was calculated for each segment for the whole 1- to 500-Hz frequency range.

Calculation of the EEG spectral power 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) to calculate the synchronization between the two signals. Coherence values (Coh) were calculated on the basis of the following formulae

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

where

\[ S_{c1,c2}(f) = \frac{1}{n} \sum_{i=1}^{n} C_1(f)C_2^*(f) \]

thus \( S_{c1,c2}(f) \) is the cross-spectrum for the EEG signal channel \( c_1 \) and the rectified EMG signal channel \( c_2 \) at a given frequency \( f \), and \( SP_{c1}(f) \) and \( SP_{c2}(f) \) are the respective power spectra for \( c_1 \) and \( c_2 \) at the same frequency. For frequency \( f \), the coherence value, \( \text{Coh}_{c1,c2}(f) \) thus corresponds to the squared magnitude of a complex correlation coefficient. \( \text{Coh}_{c1,c2}(f) \) is 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)

\[ CL(\alpha) = 1 - (1 - \alpha)^{\frac{1}{n}} \]

where \( n \) is the number of segments and \( \alpha \) is the desired level of confidence. We considered coherence to be significant over the upper 95% confidence limit.

We focused on the strongest coherences that were between the EEG channels over the left sensorimotor area contralateral to the right index finger movement and the rectified EMG.

Performance

The target force (TF) and the force exerted by the subject (EF) were filtered off-line (band-pass filter of 0.5–30 Hz) to eliminate offsets accumulated during the recording. The high 30-Hz cut-off was selected to avoid power supply artifacts and was large enough to record the changes of the force applied to the ring.

To evaluate the performance of the subjects, we calculated the error \( E \) between the TF and the EF

\[ E = TF - EF \]

Since the force generated by the manipulandum was the reference to which the subject had to adapt, we calculated the mean squared error (MSEi) of the subject force (EF) around its reference (TF) with the following formula

\[ \text{MSE}_i = \frac{\sum_{k=1}^{n} (E_{k,i})^2}{s} \]

where again \( i = 1 \ldots n \) is the segment number, \( k = 1 \ldots s \) is the sampled point in the actual segment \( i \), and \( s = 512 \) is the number of sampled points in each segment.

A measure of cumulative mean squared error, MSE, can be obtained by adding individual segment values

\[ \text{MSE} = \sum_{i=1}^{s} \text{MSE}_i \]

Statistical analysis of the performance

We first used a one-way ANOVA analysis that included two levels (static and dynamic force) to find any significant performance difference within the group of controls and between the two conditions. We compared the performance of the patient to that of the controls through 99% confidence intervals (CIs) established from the group of controls (within or outside the range).

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

\[ f(\text{MSE}) = \log(\text{MSE}) \]

Statistical analysis of SP and coherence

To test for any statistical difference between patient and controls on CMC and spectral power (either EEG or EMG), we measured the area under the coherence curve and above the significance level, \( A_{\text{coh}} \) and under the spectral power curve, \( A_{\text{pow}} \), in between two frequency windows: 15–30 Hz for beta-range and 30–45 Hz for gamma-range.

Individual values for the area of the coherence were first transformed logarithmically according to the formula
Individual values corresponding to EEG or EMG SP were normalized by using the simple logarithm

\[ A_{\text{coh}}' = \log(0.01 + A_{\text{coh}}) + 2 \]

These steps prepared the data for the application of an ANOVA analysis allowing between- and within-factors with normal distribution.

As in the analysis of the performance, we first tested for any significant difference within the group of controls using an ANOVA test, which in this case consisted of two factors “frequency” and “contraction,” each of them made up of two levels. The former factor contains the levels “beta” and “gamma,” while the latter contains “static” and “dynamic.” Significant differences of CMC and SP between the controls and the patient were well assessed through 99% CIs established from the group of controls.

RESULTS

Performance

The task was quite difficult for patient GL. We observed her performance as she carried out the task and observed 1) that she had difficulty keeping her index finger in the ring and pressing only vertically, and not laterally as well, and 2) that she often was stiffening her finger.

Figure 2 shows the performance for a single control subject (S1) and for patient GL. One can see that the patient has larger performance error for both conditions. The MSEs between EF and TF of the six control subjects and the patient are shown in Fig. 3, where it can also be seen that the patient has larger performance error for both conditions.

The ANOVA analysis for the group of six controls showed no significant difference between the static and dynamic condition. In contrast, the patient in both conditions has a performance error (MSE static: 4.52; dynamic: 5.20) that is above the 99% CIs calculated on the controls (static: [2.74, 4.35]; dynamic: [3.63, 4.34]). This indicates that the task was more difficult for the patient to perform in both conditions.

CMC

In both conditions, we found significant coherence. However, significant differences in CMC were found between the two conditions and between controls and the patient. Figure 4 shows original coherence curves of all control subjects for both static and dynamic conditions. As can be observed, during the static condition, the most prominent coherent activity is confined to the beta-range. During the dynamic condition in contrast, the highest coherent activity occurs now in the gamma-range and the beta CMC is abolished. This pattern of activation was shown to be significant within the group of controls as disclosed by the interaction condition x frequency band \[ F(1,20) = 9.14, P = 0.0067 \] of the two-way ANOVA analysis performed.

In contrast, patient GL had different activation patterns (cf. patient in Fig. 4). During the static condition, significant coherence in the beta-range was found with one single peak at
23.4 Hz and with an amplitude of 0.018. During the dynamic condition, no gamma-range CMC but a coherent peak in the beta-range with the same amplitude as for the static force at 25.4 Hz was observed.

Figure 5A shows the individual significant CMC values for static and dynamic conditions. As can be observed, all six controls who took part in this study presented increased values of CMC in the beta-range during the static condition. During this condition, some subjects presented gamma-range CMC but not of higher magnitude than that appearing in the beta-range. This beta-range coherence outgrew the gamma-range coherence in all subjects. Except for subject 5, who had a maximum level of coherence of 0.07 at 29.3 Hz, the maximum beta-range coherence across subjects ranged from 0.012 to 0.035 (peak values). The CMC values for the patient, represented by a square in Fig. 5A, are not different from those of the controls during the static condition.

During the dynamic condition, the maximum CMC values ranged from 0.01 to 0.03 (peak values). Subject 5 also presented very low-magnitude beta-range CMC, but overall, the beta CMC was significantly decreased compared with the static condition and the highest CMC activity for all controls was found in the gamma-range. The patient, in contrast, had only beta-range CMC, and her value, 0.3, lies outside the 99% CI [0.072] calculated from the control group during the dynamic condition. However, the patient’s beta-range CMC was actually inside the confidence interval [0, 0.9] of the control group during the static condition.

Cortical spectral power (SP)

To test whether the local cortical power (i.e., the amount of neurons firing in synchrony) is also modulated by the condition, we computed the cortical motor spectral power over the left motor cortex. Figure 6 shows the original SP curves of all subjects for both conditions. Nevertheless, a decrease in the amplitude of the beta-range cortical power can be observed in the dynamic condition. When we analyzed the cortical SP for all control subjects, no significant differences between the two conditions, neither in beta nor in gamma SP, could be found.

However, the ANOVA analysis showed that the within-factor “frequency band: was significant [F(1,20) = 8.68, P = 0.008], indicating that the SP in the beta-band remains higher than that in the gamma-band in both conditions. We calculated the 99% CIs for SP within the group of controls and observed that, during the dynamic condition, patient GL had significantly increased power in the beta- and gamma-band (beta, 2.87; gamma, 2.67) compared with the control subjects (beta: [1.68, 2.60]; gamma: [1.51, 2.21]). This can also be observed in the individual values for the controls and the patient displayed in Fig. 5B.

EMG spectral power

We also studied the motor unit synchronization as reflected in the SP of the rectified EMG. We found that the EMG SP was significantly increased during the dynamic conditions as indicated by the within-factor “Condition” [F(1,20) = 4.98, P = 0.037]. The patient, however, presented much higher EMG power values during both conditions (cf. Figs. 7 and 5C). The 99% CIs for the group of controls were defined for the static condition (beta: [0.25, 1.60]; gamma: [0.15, 1.53]) and for the dynamic condition (beta: [0.30, 2.60]; gamma: [0.23, 2.47]). EMG power for the patient was clearly outside this range in the static (beta: 2.71; gamma: 2.66) and dynamic conditions (beta: 2.73; gamma: 2.65).

DISCUSSION

In a previous study (Omlor et al. 2007), we investigated CMC and showed that, in contrast to the generation of static force that is accompanied by beta-range (15–30 Hz) synchronization, gamma-range (30–45 Hz) CMC is dominant during dynamic force. We hypothesized that, during dynamic force, the sensorimotor system resonates at gamma-range frequencies to rapidly integrate the visual and proprioceptive information needed to produce the appropriate motor command. This study showing that the deafferented patient GL has no gamma-range coherence during dynamic force output enhances our knowledge on the role of afferent inflow in coherence with the novel finding that proprioceptive feedback is mandatory for the genesis of gamma-range CMC during dynamic force motor output.

The participation of peripheral afferent information in the beta-band CMC has been addressed by manipulating nervous conduction delays using arm cooling (Riddle and Baker 2005), digital nerve anesthesia (Fisher et al. 2002), or ischemia as a transient deafferentation technique (Pohja and Salenius 2003). In the first case, Riddle and Baker showed that coherence phase was nonlinearly modified with cooling. In the two other studies, CMC was reduced but not abolished. Although afferent inflow may modulate beta-range CMC, our results reconcile the view that the efferent motor information alone is sufficient to generate beta-band CMC during steady-state force. Recently Gerloff et al. (2006), by clearly identifying the primary motor and somatosensory cortex in patients with early brain lesions, also provided evidence that beta-range CMC represents efferent drive from the primary motor and not reafferent feedback processing. This is also in line with Farmer et al. (1993), who studied synchronization between single motor units in the first dorsal interosseous muscle of the dominant (right) hand of another deafferented patient (IW) and did not report any
significant differences between deafferented and control sub-
jects. However, Kilner et al. (2004) have recently found, in the
same deafferented patient (GL), very low levels of EMG-EMG
coherence between different hand muscles during a contraction
task on compliant objects (where both thumb and index fingers
are involved in an isometric muscle contraction). This seems to
be in disagreement with Farmer et al. (1993). Kilner et al.
(2004), however, suggested that there is no real inconsistency
between very low levels of coherence across different hand
muscles and oscillatory motor drive synchronizing motor unit
activity within a single muscle. The cortical synchronization
may be insufficient to couple several hand muscles but strong
enough to provide motor unit coupling within one muscle.
Thus it may not be surprising that, in this study, motor cortical
synchronization driving the forearm flexor, prime mover in the
task, was present in patient GL. However, this basic CMC in
patient GL cannot be modulated either by force compliance
(Kilner et al. 2004) or during isometric compensation of
dynamic forces as shown by this study. It must be noted that
the levels of CMC that we found for both patient and controls
are actually lower in magnitude as those we obtained previ-
ously (Omlor et al. 2007) under the same conditions for a
younger group of subjects (mean age, 29 ± 13 yr). It is thus
possible that age is a factor that can modulate CMC, and we
aim to clarify this in future studies.

Kilner et al. (2004) also found that patient GL presented no
difficulties in performing the task under visual control and that
her performance was comparable with that of the control
subjects. This may be in apparent contradiction with our
results, but it is worth mentioning that, in a previous study of

FIG. 4. Frequency-coherence plots for EEG-EMG coherence during static force (left) and dynamic force (right) for all control subjects and for patient GL. 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 patient presented only beta-range corticomuscular coherence (CMC) during the dynamic condition.
FIG. 5. Individual values. A: CMC coherence (cumulated area over confidence level), in beta and gamma-range, for the 6 healthy subjects (circles numbered 1–6) and the patient (square) during static (left) and dynamic (right) conditions. Empty markers, values for the beta-range; filled markers, values for the gamma-range. Note that the patient presented only beta-range CMC during the dynamic condition. B: individual EEG spectral power values with same plotting conventions as in A. Note the higher power values in the beta- and gamma-band during the dynamic condition for the patient. C: individual EMG spectral values with same plotting conventions as in A. Note the increased power in patient GL during both static and dynamic conditions.
ours on the control of isometric force in precision grip, we did not find any significant difference in performance between patient GL and the controls (Patino et al. 2006). In contrast, our present visuomotor task required the quasi-isometric compensation of vertically applied forces on the index finger, a task that is quite dependent on proprioceptive information, particularly in the case of dynamic force modulations. Since the patient could only use the visual feedback on the screen, she had difficulties to press the ring in a vertical-only direction and adjust her force. Therefore the lack of somatosensory information made the task very demanding for patient GL, and her performance was found to be significantly worst than that of the control group in both conditions. Concurrently, her performance was accompanied only by beta-range CMC. Thus the patient does not show CMC modulation because her beta-range CMC remains unchanged from static to dynamic condition, i.e., from a simpler to complex task.

With respect to the gamma-band, integration of afferent inflow has also been postulated. Cortical gamma coherence has been observed during consciously perceived electrical stimuli applied to one hand and was absent for nonperceived ones (Meador et al. 2002). This suggests that gamma-band coherence does play a role during somatosensory detection tasks. Bauer et al. (2006) also reported that spatial tactile attention increased and prolonged gamma-band activity in the somatosensory cortex. It might be argued that it is impossible to disambiguate in the generation of gamma-band CMC the role of bad performance and of absence of proprioception. We have indeed shown that higher CMC is related to better performance (Kristeva et al. 2007). However, the control of dynamic forces in our task is complex because it requires the continuous tracking of a periodically modulated force, using both proprioception and a visual feedback. In Omlor et al. (2007), we suggested that the control of dynamic forces may be associated to several cognitive factors also, principally the allotment of...
higher attention resources to anticipate the dynamic force modulations and plan the motor output accordingly. Nevertheless, in our task, readiness to respond and motor planning are processes mostly dependent on the proprioceptive feedback. Cutaneous and joint receptors, tendon organs, and muscle afferents provide information on the strength of the force and in particular on the rate of force change. Both parameters cannot be obtained directly from the visual feedback. Indeed, it has been shown that “the discharge of afferents in response to mechanical fingertip events provides information about these events fast enough to account for the use of tactile signals in natural manipulation” (Johansson and Birznieks 2004). Furthermore, cutaneous tactile afferents are capable of triggering an appropriate change in exerted force in response to an imposed change in load force, whereas muscle and joint afferents may provide information related to the reactive forces produced by the subject (Macefield and Johansson 1996). To summarize, for the control of dynamic forces in our task, afferent information is required to plan the adequate motor output, which, accordingly, will be translated into a better performance. In this sense, proprioceptive information and performance are tightly related to the generation of gamma-band CMC.

In the absence of peripheral sensory information, only the visual feedback remains. As previously indicated in Omlor et al. (2007), greater demands on the motor cortex, more variable over time and depending on focused attention, are accompanied by gamma-band CMC, in contrast to simple isometric static forces (Brown 2000; Mima and Hallett 1999; Schoffelen et al. 2005). Accordingly, patient GL could have been expected to show a CMC modulation in the gamma-range even based on visual feedback alone in the more demanding dynamic task. However, visual feedback alone is not sufficient to perform the present dynamic force task as is shown by the high imprecision of patient GL when tracking the externally imposed force modulations. The high MSEs of her force curves

**FIG. 7.** EMG spectral power during static force output (left) and during dynamic force output (right) for all subjects and for patient GL. The beta-range (15–30 Hz) is marked in light gray and the gamma-range (30–45 Hz) in dark gray. Note the increased power in patient GL during both static and dynamic conditions.
very clearly showed her difficulties in performing the task. The frequency of the force change is certainly too high for her to isometrically compensate the sinusoidal modulations based on the visual feedback only, as she did on a lift-weight task (Fleury et al. 1995) and for simple isometric contraction (Patino et al. 2006). Occasionally, patient GL compensated the lack of proprioceptive information by increasing stiffness in her index finger to inhibit uncontrolled finger movements and circumvent the exact tracking of the force modulations exerted by the manipulandum. This could also explain her high levels of EMG and cortical power principally in the beta-band and suggests that GL uses a different strategy in the task. Indeed, it has been suggested that elevated beta-synchrony might herald a cortical state, albeit temporary, in which any processing of new movements is impaired (Gilbertson et al. 2005). As a consequence, the corticospinal network resonates at lower frequencies to perform a task with immutable force output. It is worth noting that the control subjects investigated in this study were age-matched to the patient and had a mean age of 50 ± 5 yr, i.e., they were older than the control group studied by Omlor et al. (2007) (age, 29 ± 13 yr). The control subjects investigated in this study showed generally lower CMC values as in our previous study (Omlor et al. 2007). Whether this effect is caused by age should be clarified in further studies.

We conclude that various mechanisms can be associated with beta- and gamma-band CMC. Coherence in the gamma-band reflects extensive sensory processing and, during the control of dynamic force, proprioceptive information is mandatory. In the absence of afferent feedback, CMC in the beta-band can operate an effenter motor mode to maintain a steady motor output during static and dynamic force.

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