Corticomuscular coherence behavior in fine motor control of force: a critical review

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Introduction. Understanding how the human motor control operates is an important issue to the neuroscience. One example is how the motor cortex controls muscle activity, which can be observed through corticomuscular coherence (CMC).

Aim. Our study aimed to verify the influence of certain factors related to the fine motor control of force tasks on CMC. Our issue is if would be possible the strength of the coupling between the central and muscular systems measured by changes in oscillatory activity of beta- and gamma-band being influenced by these factors as much healthy subjects as patients.

Development. Beta-band CMC was especially important when executing sustaining accurate control tasks, which need more concentration and effort. However, we found that beta-band CMC was influenced by some factors. With regard to gamma-band CMC, apparently a complex and continuous dynamic integration of several mechanisms would be necessary to modulate gamma-band CMC, since it was not modulated by magnitude of force. Therefore, it seems these mechanisms would be required to an adequate and effective neural networks operation when a dynamic force output is required.

Conclusion. Beta- and gamma-band CMC could enrich our understanding of the dynamic changes of the motor system not only in health subjects but also in neurological patients. It may serve as a sensitive index for quantifying dynamical changes in fine motor control of force. It has the potential to become a useful tool to characterize the patterns of changes in central nervous system's activities for the purposes of basic research, especially in restoring of motor function.

Key words. Beta-band. Corticomuscular coherence. Fine motor control. Force. Gamma-band. Sensorimotor integration.

Introduction

Understanding the network of the human motor control system is an important issue in integrative neuroscience. One example is how the motor cortex controls and regulates muscle activity. This is possible through the sensorimotor integration process. Sensorimotor integration is the continuous processing, by the motor system, of sensory afferents in order to prepare motor acts and to improve the execution of fine motor tasks. In this process, the central nervous system (CNS) integrates information coming from multiple sensory channels, allowing the performance of specific, goal-directed tasks, such as force tasks [1-3].

With this in mind, the relationship between cortical activity and muscular force has been carefully investigated in neurophysiology of motor control [4-7]. Such fact is possible due to a method called corticomuscular coherence (CMC) that measures the oscillatory activity of brain signals, which are coupled with muscle activation in several different frequency bands, depending on the functions and tasks engaged within the motor system. The importance of CMC becomes evident by a brief observation at experiments in sensory neurophysiology that have demonstrated the functional relevance of neuronal oscillatory activities and their synchronization in information processing. Temporal correlation between spatially distinct neural networks, mathematically expressed as coherence, it was proposed to be a neurophysiologic correlate of functional coupling between them [8,9].

With regard to this, coherence is 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 using the following formulae:

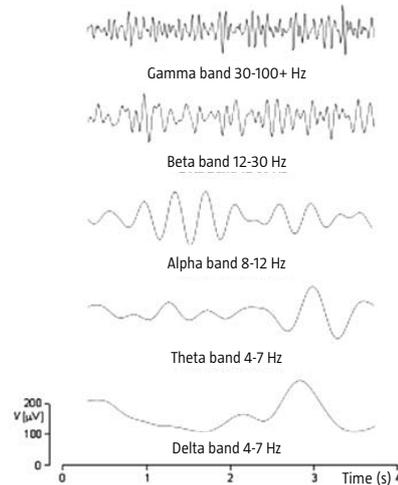$$Coh_{c1,c2}(f) = \frac{|S_{c1,c2}(f)|^2}{|SP_{c1}(f)| \times |SP_{c2}(f)|}$$

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

where Sc1,c2(*f*) is the cross-spectrum for the EEG signal channel c1 and the rectified EMG signal in channel c2 at a given frequency *f* and SPc1(*f*) and SPc2(*f*) are the respective power spectra for c1 and c2 at the same frequency. For frequency *f,* Coh(c1,c2)(*f*), thus corresponds to the squared magnitude of a complex correlation coefficient, which Coh(c1,c2)(*f*) is then a real number between 0 and 1 [10].

It is knowledge that the entire motor system, from intention to action, involves and requires a strong communication. Therefore, CMC is a link of a chain of the motor network when cortex communicates with the muscle. Furthermore, due to coherence is a correlation between two oscillatory activities, this analysis might imply that the frequency where coherence occurs is a common timer frequency of the motor command processing [10]. In line with that, voluntary motor performance is a result of the cortical command driving muscle actions. The cortex-muscle coherence is of interest for understanding of cortical control of voluntary movements and the pathophysiology of various motor disorders, as well as for unraveling the functional significance of cortical rhythms. Analysis of the CMC can provide a useful tool for understanding the corticomuscular connection in movement disorders patients. The unparallel changes of the signals between the cortex and muscle suggest decoupling of these two signals. However, the fine motor control of force-related CMC has never been directly investigated. Therefore, understanding this phenomenon would help better elucidate certain mechanisms related to movement disorders and develop or implement therapies for treating these clinical populations. In addition, the better understanding of this issue could enrich our knowledge about neuroplasticity of the motor system, not only for healthy subjects, but mainly for neurological patients.

Although the physiological basis of CMC has been far from clear, it is now generally accepted that CMC reflects communications between the brain and muscle, which is considered to be related to controlling force [11]. Abnormal features of CMC have been reported in movement disorders, such as stroke [12], suggesting impairments in corticomuscular communication in the patients. The purpose of this study was to verify the influence of certain factors (i.e., magnitude of force, attention resources, afferent mechanisms and task complexity) related to the fine motor control of force tasks (i.e., finger- and hand-grip tasks) on CMC. Our issue is if would be possible the strength of the coupling between the central and muscular systems measured by changes in oscillatory activity of beta-

and gamma-band being influenced by these factors as much healthy subjects as patients.

Methods

The present paper reviewed the CMC in static and dynamic force output in healthy subjects and neurological patients. According to above topics, we developed a strategy for searching studies in the main data bases. The computer-supported search used the following databases: Pubmed/Medline, ISI Web of Knowledge and Scielo. The search terms 'beta-band', 'corticomuscular coherence', 'CMC', 'dynamic force', 'electromyography', 'EMG' 'electroencephalography', 'EEG', 'gamma-band', and 'static force' were used and those of internationally renowned experts in this field. Only papers, such as, critical and systematic reviews, meta-analyses and experimental reports published in English and conducted from 2002 up to 2009 were preferentially reviewed. The inclusion criteria for the studies related to questions were:

– Right-handed healthy and patient subjects.
– Static or dynamic force tasks (i.e., finger- and hand-grip tasks) involving attention resources (i.e., visual stimuli, stimuli competition and arithmetic task), afferent mechanisms (i.e., tactile and proprioception), force magnitude (i.e., force levels) or task complexity (i.e., level of precision task).

Figura 2. a) CMC in static force output for healthy subjects; b) CMC in dynamic force output for healthy subjects.
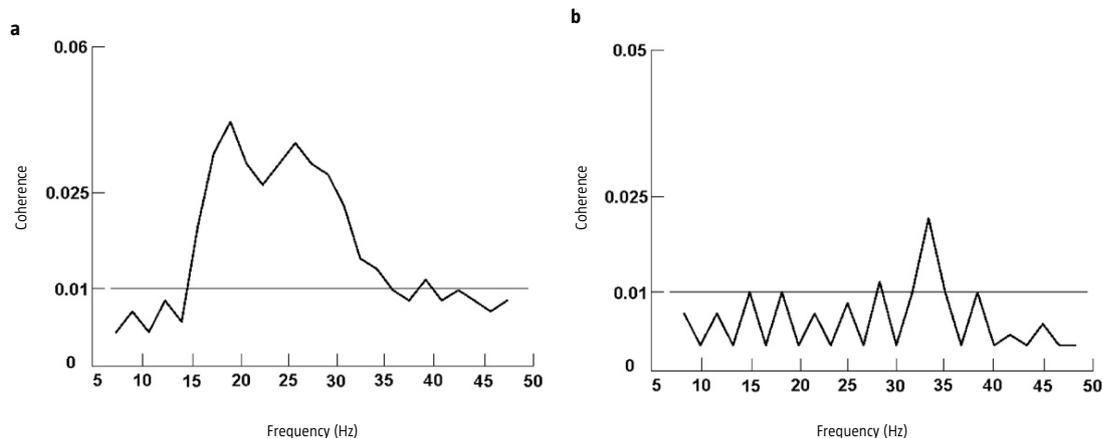
– Task performance expressed not only in EEG-EMG data (i.e., beta- or gamma-band CMC) but also in behavioral data (i.e., error measures).
– Data acquired on contralateral primary sensorimotor area or cSM1 (i.e., C3 electrode).

CMC in static and dynamic force output in healthy subjects

The term 'brain wave' in fact indicates that the electromagnetic brain activity is oscillatory in nature, as can be observed in figure 1. In healthy awake subjects, EEG confirms the beta- and gamma-band activity mainly over SM1 at 15 to 35 Hz [13,14]. Two major factors that can affect the CMC have been reported, i.e., the muscular force and the movement type (i.e., tonic versus phasic). In line with this, studies demonstrated that for maximum voluntary contraction (i.e., strong contraction), during slow movements [15], and during or just after phasic movements [16], CMC within the gamma-band can be observed [17,18]. On the other hand, within the weak to moderate tonic contraction, and during fast movements, CMC is generally entirely in the beta-band [13,14].

In force tasks, the static motor output is characterized by synchronization between oscillatory cortical motor and muscle activity confined mainly to the beta-band (15–30 Hz), as observed in figure 2a [19-22]. The strong coupling to muscles also implies the view of the SM1 as an integrative operator which controls force output [23], essential for rehabilitation

of movement disorders. There are many experiments that found opposite results, while gamma-band CMC was found during maximal and submaximal force levels [17], beta-band CMC (15-30 Hz) is restricted to periods of weak to moderate maintained tonic contractions [15,17,18,21,22,24-27]. However, this beta-band CMC shows clear task dependence, occurring only during the hold phase while being abolished during the ramp phase of a precision grip task [11,15,27,28]. Several studies have demonstrated that beta-band CMC is modulated by afferent information [29-33] and visuomotor tasks [34].

On the other hand, in force tasks the dynamic motor output is characterized by synchronization between oscillatory cortical motor and muscle activity confined to the gamma-band (30-45 Hz). In the dynamic condition, the most distinct CMC occurs in the gamma-band while beta-band is markedly reduced, as observed in figure 2b. It is also hypothesized that for the control of dynamic forces, the sensorimotor system resonates at gamma-band to rapidly integrate the visual and proprioceptive information and produce the appropriate motor command [35]. Thus, the functional role of the mechanisms that interfere on synchronization between oscillatory cortical motor and muscle activity are still unclear.

Within this context, some studies demonstrated that beta-band CMC can be modulated due to different factors related to the fine motor control of force such as, different magnitude of force (i.e., force levels) [14], attention resources, i.e., visual stimuli [22,36], stimuli competition and arithmetic task [37], and task complexity, i.e., level of precision

Table I. CMC in static force output in healthy subjects.

	Objective	Sample	Protocol	Main results
Kristeva-Feige et al [22]	To investigate whether beta-band CMC on C3 electrode varies with the attention resources (i.e., arithmetic task) and task complexity (i.e., precision of the exerted force).	n = 10	Subjects were required to maintain a constant isometric force by pressing a force transducer with his dominant index finger starting from complete resting state. Visual feedback related to force level was given by an analog display in front of each subject. The exerted force was 8% MVC for each subject as established prior to start the task. Three different conditions were investigated: – Performing the task with HP. – Performing the task with HP and simultaneously performing a mental arithmetic task (i.e., HPAT, subtracting 7 sequentially starting from 200, 300 or 400), i.e. attention was divided between the motor task and the mental arithmetic task. – Performing the task with LP, 20% around the force level of 8% MVC.	It was found that beta-band CMC in the HP condition was confined to 28 Hz. In the LP condition the beta-band CMC was confined to 24 Hz, which is lower than HP condition. Such fact also seems to occur in the beta-band CMC in the HPAT condition due to the higher level of attention associated with the motor task. It was observed that beta-band CMC represents a state of the cortico-muscular network when attention (i.e., visual stimuli) is directed towards the motor task. Such fact is associated with, and possibly encodes, precision in force production.
Safri et al [36]	To investigate the beta-band CMC on C3 electrode varies with the attention resources (i.e., visual stimuli) during an isometric task between the conditions with and without distractive visual stimulation.	n = 9	Subjects were asked to hold a device with a force gauge sensor at its center between the thumb and the index finger, and to squeeze the device to cause a weak contraction (i.e., ~15% MVC). The first experiment was composed of before, visual task and after conditions. The control conditions (i.e., before and after) required the subject to maintain the muscle contraction without visual stimulation. In this task, subjects were asked to ignore the stimuli during the muscle contraction.	It was found a significant beta-band CMC increased in magnitude in the visual task condition when compared with the control conditions. The results suggested that CMC reflected a cognitive effort needed to maintain an isometric constant force when visual stimuli need to be ignored, enhancing the cognitive effort and CMC.
Safri et al [37]	To investigate the beta-band CMC on C3 electrode to investigate the attention resources (i.e., visual stimuli, stimuli competition and arithmetic task), i.e., the brain's division in attention during a motor task, and the effects of division and no division in attention on a force task with visual stimulation	n = 10 (experiment 1) n = 5 (experiment 2)	Subjects were asked to hold a device with a force gauge sensor at its center between the thumb and the index finger, and to squeeze the device to cause a weak contraction (i.e., ~10 % MVC). The first experiment was composed of before, task (i.e., visual task: Ignore or Count) and after conditions. The control conditions (i.e., before and after) required the subject to maintain the muscle contraction without visual stimulation. In this task, subjects were asked to ignore the stimuli and to count certain stimuli during the muscle contraction. The second experiment was performed in the same pattern, but it was used an arithmetic task (i.e., AT task), where the subjects were asked to perform a simple subtraction.	It was found a significant increase in magnitude of beta-band CMC for the Ignore and Count conditions as compared with before and after conditions. In addition, it was noted a significant decreased in magnitude of beta-band CMC for the AT condition as compared with the control conditions. It was found that beta-band CMC is sustained/enhanced during isometric contraction in the presence of visual stimulation which may be facilitated by the attentional suppression of the visual stimuli irrelevant to the motor task and suppression of the attended stimuli processing.
Witte et al [14]	To investigate if an increase in the magnitude of static force output (i.e., force levels) is associated with enhanced beta-CMC on C3 electrode.	n = 8	Subjects had to periodically modulate dynamic isometric force output (i.e., 4% and 16% MVC) produced by a manipulandum. As a visual feedback of the force level, subjects had to keep a visual cursor within a target zone with their right-index finger.	It was found a significant increase in CMC amplitude from 4 to 16% MVC in beta-band being associated with a better performance (i.e., revealed smaller relative errors). It was demonstrated that beta-band CMC may serve as an effective sensorimotor integration process through a stronger binding between cortical and motor neurons to stabilize corticospinal communication during isometric compensation of low-level static forces.
Kristeva-Feige et al [19]	To investigate whether beta-band CMC on C3 electrode varies with the task complexity (i.e., precision of the exerted force).	n = 8	Subjects had to periodically modulate dynamic isometric force output (i.e., 4% MVC force) produced by a manipulandum. As a visual feedback of the force level, subjects had to keep a visual cursor within a target zone with their right-index finger.	It was found an increase in the amplitude in beta-band CMC related to the task performance, i.e., the error signal between target and exerted force. This finding suggests an effective corticospinal interaction through static force and precision grip task.

CMC: corticomuscular coherence; MVC: maximum voluntary contraction; HP: high precision; LP: low precision.

task [19,22], as observed in table I. On the other hand, other studies demonstrated that gamma-band CMC (30-45 Hz) has been associated with isometric compensation of low dynamic force (4% MVC), and may function to provide rapid integration of attention resources (i.e., visual stimuli), and afferent mechanisms (i.e., tactile and proprioception information) [13,38], besides the well-documented significant beta-band CMC with the exception of the study of Chakarov et al [39] that found a significant broad-band CMC (15-45 Hz) comprising both beta- and gamma-band related to the force level. It was not found any significant modulation in gamma-band CMC regarding magnitude of force (i.e., force levels) [13,38,39], as observed in table II.

CMC in static and dynamic force output in movement disorder' patients

In the field of motor control, it is a fundamental problem to quantify the brain signal that modulates the force in a fine motor control task such as handgrip. Within this context, much attention has been given to the functional organization of the corticospinal system and the mechanisms of muscle control by the CNS and in particular to the universal mechanism of neuronal interaction via synchronization, which plays a relevant role in the effective coordination between the cortical motor areas and the muscles. With regard to this, it is important and necessary to understand the functional coupling between cortical commands and consequent muscle activation in movement disorders. It is knowledge that motor deficits are a major consequence of several movement disorders, such as stroke. Though, it is generally believed that these disorders interrupts or damages the neural networks that control movements. Moreover, little is known regarding the influence of different factors related to the fine motor control of force tasks on CMC in movement disorders.

Within this context, Patino et al [35] investigated and demonstrated that for the control of dynamic forces, afferent information is required to plan the adequate motor output, giving support that afferent mechanisms (i.e., proprioceptive information) are mandatory in the genesis of gamma-band CMC during the generation and the control of only dynamic forces. Healthy subjects presented significant gamma-band CMC, in contrast to neurological patient. Moreover, Patino et al found only the well-documented significant beta-band CMC for both healthy subjects and neurological patient (Figures 3a and 3b, and Table III).

Discussion

The purpose of this study was to verify the influence of certain factors (i.e., magnitude of force, attention resources, afferent mechanisms and task complexity) related to the fine motor control of force tasks (i.e., finger- and hand-grip tasks) on CMC. Our issue is if would be possible the strength of the coupling between the central and muscular systems measured by changes in oscillatory activity of beta- and gamma-band being influenced by those factors as much healthy subjects as patients. It was verified that beta-band CMC was influenced by several factors in contrast to gamma-band CMC. Within this context, the discussion is divided into subsections, where we will discuss the role of each factor in fine motor control of force.

Attention resources

When observed the attention resources, the beta-band CMC decreases significantly when the attention is divided between the motor task and another simultaneously performed task, i.e., this finding suggest that beta-band CMC may reflect attention towards the motor task. Such fact was observed when subjects performed the isometric contraction with concurrent mental arithmetic (i.e., higher cognitive effort) [22,37]. Furthermore, the finding that beta-band CMC decreases when attention is divided supports the view that it plays an active role in motor control [11,15,40] and does not reflect 'idling rhythm' as originally suggested [41,42]. Within this context, the beta-band CMC was regarded as an indicator of efficient motoneuron recruitment associated with a minimum of computational effort [28,43].

On the other hand, when the attention is divided between the motor task and another simultaneously performed task, no decrease (i.e., increase) in beta-band CMC when subjects needed to attend to both visual stimulation and motor action (i.e., count condition; lower cognitive effort) [22,36]. Furthermore, it was found enhanced beta-band CMC when no attentional division was needed (i.e., ignore condition; without cognitive effort) [22,36, 37]. Any change in the beta-band CMC was due to force level when subjects performed the isometric contraction with equal force. The level of attention given to the isometric contraction task, e.g. total, reduced or no attention probably caused the variation in the beta-band CMC (i.e. increased or decreased). Recently, beta-band CMC was shown to depend on the difficulty of performance of the motor task [44]. Therefore, if cognitive effort must be

Table II. CMC in dynamic force output in healthy subjects.

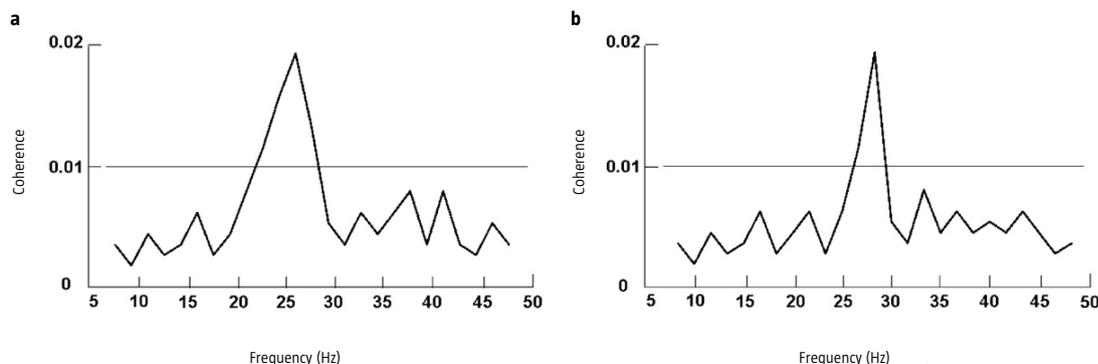|	Objective	Sample	Protocol	Main results
Omlor et al [13]	To investigate if the magnitude of dynamic force output (i.e., force levels) requires a more complex sensorimotor processing and thus being accompanied by oscillations at gamma-band CMC on C3 electrode.	$n = 8$	Subjects had to periodically modulate dynamic isometric force output (i.e., 4% MVC force) produced by a manipulandum at a frequency of 0.7 Hz and with peak-to-peak amplitude of 1.6% MVC. As a visual feedback of the force level, subjects had to keep a visual cursor within a target zone with their right-index finger.	It was found a significant increase in gamma-band CMC in the dynamic condition. These findings demonstrated 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.
Andrykiewicz et al [38]	To determine whether the magnitude modulation of dynamic force output (i.e., force levels) has an influence on the gamma-CMC on C3 electrode.	$n = 8$	Subjects had to periodically modulate dynamic isometric force output (i.e., 4% MVC force) produced by a manipulandum. The task was composed of three different experimental conditions: – Static force condition. – Small dynamic force condition, at a frequency of 0.7 Hz and with peak-to-peak amplitude of 1.6% MVC. – Large dynamic (force condition, at frequency of 0.7 Hz and with peak-to-peak amplitude of 4% MVC.	It was found no significant gamma-band CMC for both small and large dynamic force conditions. It was suggested that a more complex and continuous dynamic integration of higher attention resources (i.e., visual stimuli) as well as afferent mechanisms (i.e., tactile and proprioceptive information) and cognitive information would be needed to modulate gamma-band CMC. These mechanisms would be required to an adequate and effective neural networks operation when a dynamic force output is required.
Chakarov et al [39]	To verify whether the magnitude of dynamic force output (i.e., force levels) interfere with the gamma-band CMC on C3 electrode.	$n = 7$	Subjects had to periodically modulate dynamic isometric force output (i.e., 4% MVC force) produced by a manipulandum at a frequency of 0.7 Hz and with peak-to-peak amplitude of 1.6% MVC. As a visual feedback of the force level, subjects had to keep a visual cursor within a target zone with their right-index finger. The task was composed of three different experimental conditions, 8%, 16% and 24% dynamic force condition.	It was found a significant modulation on gamma-band. On the other hand, it was found a broad-band CMC comprising both beta- and gamma- band. It was suggested that sensorimotor system may request for a stronger and also broader beta-band CMC to produce stable corticospinal interaction during increased force level, as well as when compensating for dynamic modulated forces. It re-enforces the significance of the beta-band CMC in sensorimotor integration process, demonstrating that not only gamma-band CMC is important to this process.

CMC: corticomuscular coherence; MVC: maximum voluntary contraction.

enhanced to maintain constant force grip during the visual stimulation, this will be reflected in enhanced beta-band CMC.

Level of precision

In relation to the level of precision, one of the studies [22] found on computer-supported search demonstrated reductions in beta-band CMC when different levels were investigated. The low precision condition differed from the high precision condition in that subjects must attend less to the accuracy of the required force. Within this context, Baker et al [27] suggest two different mechanisms for generation of the oscillations in the motor system. The first one may be the presence of chattering cells similar to those described in the visual system [45] with intrinsic membrane properties leading to periodic bursting behavior with the inter-burst frequency ranging from 20 to 70 Hz. In the case of such cells exist in the motor cortex they could be responsible for the beta-band oscillations. The second mechanism proposed by Baker et al [27] is a dynamic network function for the generation of the oscillations which is shown to be dependent on the activity of the inhibitory interneurons. Changes in the inhibitory conduction delays and in the time course of inhibitory postsynaptic potentials both could affect a frequency shift of the network oscillations. Having in mind these two mechanisms, the different beta-band CMC between the low and high precision conditions may be due to precision-modulated intrinsic cell properties of the chattering cells and/or to precision-modulated changes in the network dynamic function paced by the inhibitory interneurons. The results indicate that both manipulations seem to modify beta-band CMC, but in two different ways, and moreover, these findings suggest that beta-band CMC is associated with, and possibly encodes, precision in force production.

Figure 3. a) CMC in static force output for neurological patient; b) CMC in dynamic force output for neurological patient.

Table III. CMC in static and dynamic force output in movement disorders' patients.

	Objective	Sample	Protocol	Main results
Patino et al [35]	To test the role of the afferent mechanisms (i.e., proprioceptive afferent feedback) in the generation of gamma-band CMC on C3 electrode during isometric compensation of dynamic forces.	$n = 6$ (age- and sex-matched controls) $n = 1$ (polyneuropathy)	Subjects had to periodically modulate dynamic isometric force output (i.e., 4% MVC force) produced by a manipulandum at a frequency of 0.7 Hz and with peak-to-peak amplitude of 1.6% MVC. As a visual feedback of the force level, subjects had to keep a visual cursor within a target zone with their right-index finger.	During dynamic force condition, healthy subjects presented a significant increase in gamma-band CMC, in contrast to the patient. It was suggested that afferent mechanisms (i.e., proprioceptive information) are mandatory in the genesis of gamma-band CMC during the generation and control of dynamic forces.

CMC: corticomuscular coherence; MVC: maximum voluntary contraction.

Moreover, when analyzed the other study [19], the increase in beta-band CMC between target and exerted force performance suggest the view that the functional significance of the beta-band CMC during static force output is to promote an effective corticospinal interaction provides a framework for the explanation of several findings: oscillations are abolished during phasic movements, and only appear when muscles are in static contraction [15,28,46], suggesting that the beta-band oscillations can represent a form of recalibration of the length tension ratio and preparing for the next movement [33,46,47]. In addition, Perez et al [34] found an increase in the beta-band CMC after visuomotor skill learning and suggested that the increased CMC reflects a tighter cortical control of the muscle activity in relation to the acquisition of the task. However, the tighter cortical control of muscle activity may reflect a more efficient corticospinal interaction.

Force level

Previous studies have shown that static force output is accompanied by beta-band CMC [11,15,16,20, 21,25,28]. According to these results, Witte et al [14] found a significant increase in beta-band CMC amplitude from 4 to 16% MVC was found, being associated with a better performance (i.e., revealed smaller relative errors). In relation to the higher CMC amplitude for 16% compared with 4% MVC three alternative interpretations can be considered:
– Larger corrective movements in the 4% MVC condition may attenuate CMC.
– The tuning of motor unit firing-rate to low beta-band could theoretically boost CMC during 16%

MVC. However, two findings argue against this hypothesis: a) motor units in the first dorsal interosseus (FDI) start firing at a mean rate of 8.4 ± 1.3 Hz and this rate increases by 1.4 ± 0.6 Hz for each 100 g force change [48]; and b) recruitment of additional motor units was the major mechanism of force production in the low-level force. Therefore, the authors assume that the mean force of 250 g during 16% MVC is most probably related to firing rates lower than 15 Hz.

– Most reasonable in our view, the amplitude increase of CMC in the low beta-band for 16% MVC as compared with 4% MVC suggests a stronger binding between cortical and motor neurons. Previous studies also found that low-frequency beta-oscillations during visuomotor tasks bind multiple cortical areas into a large-scale network and are particularly suitable to promote effective information processing [9,49].

In the framework of effective processing, it is important to emphasize that higher beta-band CMC was accompanied by better motor performance. This proved to be true for 16% MVC, as reflected in the smaller relative error in force compared with 4% MVC. Moreover, within each condition period of lower absolute error tended to be associated with higher beta-band CMC. This is in line with the recent study of Kristeva et al [19], showing significantly higher values of beta-band CMC with good performance. This relationship also proved to be true for the other extreme: lack of peripheral feedback, e.g. in a deafferented patient [50], impaired CMC and performance. These findings suggested that the increased CMC amplitude in conjunction with the decreased performance error is a functional correlate of an effective communication between SM1 and muscle. In summary, it was shown an increase of beta-band CMC from 4 to 16% MVC and likewise within each condition from periods of 'bad' to 'good' performance. This increased CMC amplitude is suggested to result in a more effective sensorimotor loop, which is reflected in best motor performance. Instead, a functional role of CMC in sensorimotor integration, as proposed by others [32,33,49,51] seems to be reasonable. These integrative processes probably serve to adjust motor performance and therefore are highly relevant for appropriate motor control.

On the other hand, it has been seen that the isometric compensation of dynamic force modulations is accompanied by a shift of gamma-band CMC. In particular gamma-band is thought to provide a mechanism for the binding together of functionally related cortical elements such as in visual attention [52], motor planning [53,54], sensory [55,56], sensorimotor as well as visuomotor integration [57,58] and cognition [59]. Compared to the static force, the exact isometric tracking of the periodically modulated force requires higher attention resources and a more complex and continuous dynamic integration of visual as well as somatosensory information. With this mind, the shift of the gamma-band CMC 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.

Regarding the role of CMC, Marsden et al [60] has been suggested that it seems to bring effectively together selected cortical elements into the motor act, tending to shift to new frequencies when different tasks are performed, despite the involvement of the same muscles. However, Omlor et al [13] clearly demonstrated that the significant shift of the gamma-band CMC is related to the different force conditions. In addition to that, Macefield et al [61] 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, it was shown by Omlor et al [13] that oscillation of corticospinal networks at gamma-band CMC might facilitate the rapid integration of tactile, proprioceptive, visual and cognitive (i.e., prediction and planning) information during isometric compensation of a dynamic force. Therefore, it was observed gamma-band CMC during a more complex, but predictable task with a periodic design. This suggests that gamma-band CMC 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 CMC in fine and precise motor control.

In line with that, the findings of Andrykiewicz et al [38] demonstrated that the amplitude of dynamic force does not modulate the gamma-band CMC. It was found that during the control of complex tasks like the experiment of Omlor et al [13], the modulation the sensorimotor system is synchronized at gamma-band to rapidly integrate visual, proprioceptive, tactile and cognitive (i.e., prediction and planning) information. Within this context, the findings of Andrykiewicz et al [38] that the amplitude of the dynamic force does not modulate the gamma-band CMC, suggesting that changes in proprioceptive input during dynamic forces in the range from 1.6 to 4% MVC were not distinct enough for this modulation. It is assumed that neurons in

motor cortex and spinal motoneurones are synchronized at gamma-band in both dynamic conditions when compared to the static force condition. Moreover, the degree of this shift was the same for both dynamic conditions, concluding that both small and large dynamic force conditions require the same level of sensorimotor and visual integration. It is in line with the similar motor performance in both dynamic conditions, revealed by the similar relative errors. Such findings were rather associated with the internal state of the sensorimotor system as supported by the unchanged relative error between both dynamic conditions.

On the contrary, the study of Chakarov et al [39] found a significant increase in a broad-band (15-45 Hz) CMC comprising both beta- and gamma-band with the force level. The previous findings about beta-band CMC when the static force level is increased from 4% MVC to 16% MVC [14] is extended for isometric compensation of increased modulated force, suggesting that beta-band CMC may serve to stabilize corticospinal communication during isometric compensation of low-level static forces. However, the results of Chakarov et al [39] favor the view that this function of beta-band CMC is not confined to or specific for low-level static forces only. In addition, the sensorimotor system may resort to stronger and also broader beta-band CMC to generate stable corticospinal interaction during increasing force level even when compensating for dynamic modulated forces.

CMC processes have shown a pervasive presence in the CNS at several levels of neuronal organization and for different cognitive processes [62]. A detailed understanding of the functional roles of CMC for different frequency bands would represent a major advance in motor control. A thorough examination of the findings reported until now suggests multiple functions rather than specific functional roles for specific frequency bands. This is in line with a one-to-many relationship where CMC in one frequency may be involved in different functions and vice versa. Moreover, the study of Omlor et al [13] has contributed to this debate showing that beta- and gamma-band CMC are observed during isometric compensation of low-level static and dynamic forces respectively. For this reason, the findings of Chakarov et al [39] further support the multiple functions of beta-band CMC, which positively correlates with the level of a dynamic modulation of force. It suggested therefore that CMC is a highly dynamic process with multiple functions and involve either specific beta- and gamma-band according to the specificities of the motor task.

Afferent mechanisms

Regarding the afferent mechanisms (i.e., proprioceptive information) Patino et al [35] found no significant gamma-band CMC during dynamic force condition for deafferented patient, however, a significant modulation for beta-band CMC was found in the static force condition. Nevertheless, patient performance was significantly worse than the controls in both conditions. Within this context, during static and dynamic force conditions, healthy subjects (i.e., control group) presented significant beta- and gamma-band CMC. Although afferent inflow may modulate beta-band CMC, the findings reconcile the view that the efferent motor information alone is sufficient to generate beta-band CMC during steady-state force. Recently Gerloff et al [63], by clearly identifying the SM1 in patients with early brain lesions, also provided evidence that beta-band CMC represents efferent drive from the M1 and not reafferent feedback processing.

In order to control the dynamic force, 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 demonstrated by Omlor et al [13], greater demands on the SM1, more variable over time and depending on focused attention, are accompanied by gamma-band CMC, in contrast to static forces [64]. It suggested by authors that to control dynamic forces it is necessary an association of several factors to anticipate the dynamic force modulations and plan the appropriate motor output. Nevertheless, in contrast to Omlor et al [13], the task used by Patino et al [35] is more complex because it requires the continuous tracking of a periodically modulated force, using both proprioception and a visual feedback to be executed. It was demonstrated that readiness to respond and motor planning are processes mostly dependent on the proprioceptive feedback, i.e., cutaneous, joint tendon and muscle information; parameters which 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 [65]. 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 [66].

In addition, it was expected that deafferented patient has been demonstrated a modulation in the gamma-band CMC even based on visual feedback alone in the more demanding dynamic task. However, visual feedback alone was not sufficient to perform the dynamic force task as was shown by the high imprecision of deafferented patient when tracking the externally imposed force modulations. In line with this finding, some studies have been observed gamma-band activity during consciously perceived electrical stimuli applied to one hand and it was absent for nonperceived ones [55]. This suggests that gamma-band CMC does play a role during somatosensory detection tasks. Additionally, Bauer et al. [56] also reported that spatial tactile attention increased and prolonged gamma-band activity in the SM1. In line with that, 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. Authors conclude that such findings give support that afferent mechanisms (i.e., proprioceptive information) are mandatory in the genesis of gamma-band CMC during the generation and control of dynamic forces. In the absence of afferent feedback, beta-band CMC can operate an efferent motor mode to maintain a steady motor output during static and dynamic force.

Conclusion and final remarks

This review is based on the main findings of the studies appropriately selected according to our strategy of search described in the methodology. According to our findings, it would be expected that beta- and gamma-band CMC modulation were being responsible for the synchronization between upper and lower motoneurons to achieve optimal fine motor control [67]. Beta-band CMC was especially important when executing sustaining accurate control tasks, which need more concentration and effort, reflecting the preferred firing rates of motor units under a specific condition. However, we found that several factors were associated with beta-band CMC, in other words, beta-band CMC was influenced by some factors, such as, magnitude of force, attention resources, and task complexity. With regard to gamma-band CMC, apparently a complex and continuous dynamic integration of several mechanisms, such as higher attention resources as well as afferent mechanisms and cogni-

tive information would be necessary to modulate gamma-band CMC, since it was not modulated by magnitude of force. Therefore, it seems these mechanisms would be required to an adequate and effective neural networks operation when a dynamic force output is required.

Hence, beta- and gamma-band CMC could enrich our understanding of the cerebral plasticity of the motor system not only in health subjects but also in neurological patients, e.g., polyneuropathy. As a final remark and perspective, the findings suggest that beta- and gamma-band CMC modulation may serve as a sensitive index for quantifying dynamical changes in fine motor control during force tasks. It has the potential to become a useful tool to characterize the patterns of changes in CNS' activities for the purposes of basic research (i.e., motor learning and control and neuroplasticity) as well as medical studies, especially in restoring of motor function, for instance, after stroke.

Further investigation is necessary for a more complete understanding of the relationship of the synchronization between cortical activity and muscular force putting emphasis on functional recovery and localized hemispheric activation. For instance, a decrease in CMC seems to indicate impaired communication between the motor control centers in the brain and target muscles responsible for making the desired movement. This impaired coupling might arise from cortical changes related to the lesion or muscular changes after pathology [56], although the later perhaps played a less significant role as the weak coupling might primarily be caused by impaired information flow from the brain to muscle [55]. Moreover, it must be clarified in further studies if age is a factor that can modulate CMC, because it was noted by Patino et al [35] that the levels of CMC presented by controls (i.e., elderly) subjects were generally lower as previously found by Omlor et al [13] when young subjects were investigated.

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Revisión crítica del comportamiento de la coherencia corticomuscular en el control motor fino de la fuerza

Introducción. Entender el funcionamiento del control motor humano constituye una cuestión importante para la neurociencia. Un ejemplo es el modo en que la corteza motora controla la actividad muscular, control que puede observarse a través de la coherencia corticomuscular (CCM).

Objetivo. El presente estudio tiene por objeto comprobar la influencia sobre la CCM de diversos factores relacionados con el control motor fino de las tareas de fuerza. Nuestro interés estribaba en averiguar si sería posible medir la solidez del acoplamiento entre el sistema nervioso central (SNC) y el aparato locomotor a través de los cambios de la actividad oscilatoria en las bandas beta y gamma influida por tales factores, tanto en personas sanas como enfermas.

Desarrollo. La CCM en la banda beta resultó especialmente importante en la ejecución sostenida de las tareas de control preciso, que demandan más concentración y esfuerzo, y constatamos que la CCM en dicha banda estaba influida por diversos factores. Por lo que respecta a la CCM en la banda gamma, su modulación requeriría en principio una integración dinámica compleja y continua de varios mecanismos, puesto que la magnitud de la fuerza no ejerció efecto modulador alguno. De lo dicho se desprende que tales mecanismos serían necesarios para un funcionamiento adecuado y eficaz de las redes neuronales cuando se necesita producir una fuerza dinámica.

Conclusión. La CCM en las bandas beta y gamma podría ampliar nuestros conocimientos acerca de los cambios dinámicos del sistema motor, tanto en las personas sanas como en los pacientes neurológicos. Se podría utilizar como un índice sensible para cuantificar los cambios dinámicos en el control motor fino de la fuerza, y tiene posibilidades de convertirse en una herramienta útil para caracterizar los patrones de cambio en las actividades del SNC en el campo de la investigación básica, especialmente en la restauración de la función motora.

Palabras clave. Banda beta. Banda gamma. Coherencia corticomuscular. Control motor fino. Fuerza. Integración sensoriomotora.