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Journal of Oral Biosciences

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Review

Cortico-muscular communication for motor control of the tongue in humans: A review

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ARTICLE INFO

Article history:

Received 7 January 2016

Received in revised form

20 February 2016

Accepted 9 March 2016

Keywords:

Magnetoencephalography

Neural oscillation

Cortico-muscular coherence

Motor function

Hypoglossal nerve

ABSTRACT

Background: Sophisticated voluntary movements of the tongue are essential to speech articulation and swallowing in humans. Voluntary tongue movements are finely controlled by communications between the cortex and tongue muscles. A large number of previous studies have reported that functional connections between the cortex and muscles are reflected by cortico-muscular coherence (CMC), which is measured between electroencephalography (EEG) or magnetoencephalography (MEG) and surface electromyography (EMG), during isometric finger movements in humans. Recent studies indicate that CMC reflects a bi-directional flow of information between the cortex and fingers, along the descending corticospinal pathway and with ascending sensory feedback. However, CMC for the tongue has not been well-studied, despite the fact that increased knowledge would be helpful in understanding cortical entrainment of voluntary tongue movements.

Highlight: CMC was recently demonstrated using whole-head MEG signals and EMG signals from both sides of the tongue. CMC was reflected over both hemispheres, for each side of the tongue, and at two frequency bands during isometric tongue protrusions: the β band at 15–35 Hz and a low-frequency band at 2–10 Hz.

Conclusion: This review provides a detailed description of the functional connection between the bilateral cortex and each side of the tongue during sustained tongue movements in humans, using CMC analyses.

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1. Introduction

Sophisticated voluntary movements of the tongue are essential to speech articulation and swallowing in humans. These fine movements are regulated by descending motor signals from the

cortex to the muscles, and by afferent sensory feedback from the muscles to the cortex. Such functional connections between the cortex and muscles have been evaluated by analyzing oscillatory synchronization between cortical activity and muscle activity, which is referred to as cortico-muscular coherence (CMC) [1,2].

In order to elucidate the cortical processing necessary for preparation and control of limb movements, movement-related cortical activity has been extensively studied using electroencephalography

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E-mail address: maezawa@den.hokudai.ac.jp<http://dx.doi.org/10.1016/j.job.2016.03.001>

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(EEG) and magnetoencephalography (MEG), which accurately reflect activity in sensorimotor areas [3–8]. Movement-related cortical fields (MRCFs) using a whole-head MEG system revealed contralateral control of limb movements by cortical information processing in the primary sensorimotor cortex (SM1), with high spatiotemporal resolution [9]. However, there are relatively few MRCF studies of tongue movements [10], which is partially due to the technical difficulties that are inherent to MRCF recordings during tongue movements. Cortical fields may be contaminated by excessive magnetic artifacts associated with muscle activity in the orofacial region, due to the short distance between the area of movement and the recording area [11]. However, recording a weak isometric movement task for CMC analyses minimizes the magnetic artifacts associated with orofacial movements when used to elucidate the central mechanism for the tongue movement task.

2. Neural oscillatory activity

Synchronization of neural activity is essential for information processing in the nervous system. Neural oscillatory activity in the human cortex has been a focus of research ever since Hans Berger reported strong rhythmic activity in a localized frequency band (alpha; α band) that modulates with opening and closing of the eyes [12]. Subsequent studies revealed that oscillatory activity in the beta (β) frequency band in the SM1 changes based on motor output [13,14] and sensory input [15] from the limbs, indicating that β -band rhythms are related to sensorimotor function. Such transient decreases and increases in oscillatory cortical activity were quantitatively defined by Pfurtscheller and Aranibar [16] in 1977 as event-related desynchronization (ERD) and synchronization (ERS), respectively.

Our recent MEG study reported that ERD/ERS in the β band (β -ERD/ERS) was also induced by electrical stimulation of the tongue, and stimulus-induced β -ERD/ERS could be suppressed during repetitive voluntary tongue movements, suggesting that sensorimotor functions of the tongue region may be coordinated through β -band cortical oscillations [17].

3. CMC as an indicator of functional connections

The amplitude of SM1 oscillatory activity within the β band changes during passive, voluntary, and even imagined movements. Moreover, β -band cortical oscillations demonstrate coherence with EMGs in the periphery during sustained motor contractions of the limbs, suggesting a possible role of direct corticospinal connections to target muscles through the direct cortical spinal pathway. Using a MEG system with a single-channel magnetometer, Conway et al. reported increased coherence between MEG signals in the contralateral motor areas and the surface EMG signal during muscle contractions [18]. There has since been extensive research on CMC during sustained contraction of limb muscles [1,2,19,20]. MEG studies have demonstrated that the frequency of CMC changes depending on the strength of the muscular contractions [21]. More recent studies using directed coherence analyses have revealed that CMC reflects the afferent ascending signal from the muscles to the cortex, as well as the efferent descending signal from the cortex to the muscles [22,23]. Mima et al. [24] reported that efferent CMC, measured with EEG, was greater than afferent CMC during finger muscle contraction. CMC is therefore a useful method for revealing functional connections between the cortex and muscles during sustained limb muscle contractions. However, CMC in the tongue region is not well-studied, and additional research would increase understanding of cortical entrainment related to voluntary tongue movements.

4. Tongue CMC

During tongue protrusion, the primary motor cortex (M1) controls movements via outputs to hypoglossal motor neurons. Laine et al. reported findings from an EEG study that single motor units recorded from the tongue muscles with needle electrodes during tongue protrusion exhibited cortical entrainment at frequencies between 15 and 40 Hz [25]. Recently, we demonstrated CMC between whole-head MEG signals and surface EMG signals from both sides of the tongue. Tongue CMC was observed in both hemispheres, for each side of the tongue, and at two frequency bands during isometric tongue protrusions: the β band at 15–35 Hz and a low-frequency band at 2–10 Hz [26,27].

4.1. Beta frequency band

Our recent study demonstrated that β -CMC was observed in both hemispheres and for each side of the tongue during isometric tongue protrusion [26], which contrasts with results detecting β -CMC only in the contralateral hemisphere for each side of the finger during bilateral finger contractions. Bilateral hemisphere β -CMC occurs because the tongue is bilaterally innervated by corticobulbar fibers via both hypoglossal nuclei. The amplitude of β -CMC was greater for the contralateral hemisphere than for the ipsilateral hemisphere, for each side of the tongue. These findings are consistent with the results of transcranial magnetic stimulation (TMS) studies demonstrating that unilateral cortical TMS elicited motor-evoked potentials (MEPs) bilaterally in the tongue, and that the amplitudes of MEPs on the contralateral side were greater than those on the ipsilateral side [28–30]. These results may reflect contralateral dominance in the functional connections from the cortex to the tongue during human isometric tongue protrusion.

In the previous study [26], time-domain analyses of β -CMC indicated that the MEG signal preceded the EMG signal for both the tongue and the finger, and that the time delay was shorter for the tongue (mean, 9.1 ms) than the finger (mean, 18.0 ms). These findings suggest that the time delay between the MEG and EMG signals depended on the pathway length between the cortex and target muscle.

4.2. Low frequency band

A previous study reported that CMC occurs at a low-frequency band during slow, repetitive finger movements [31]. The authors concluded that CMC at the low-frequency band (low-CMC) reflects the neural mechanisms of intermittent motor control, providing common timing for synergistic muscles. Recent corticokinematic coherence (CKC) studies have also detected synchronization between the cortex and finger in the low-frequency band during slow, repetitive finger movements [32–34]. Pittulainen et al. reported a minimal contribution by active movement towards CKC at the frequency of finger movement [32], since both active and passive finger movement tasks resulted in significant CKC without any consistent spatial difference in the source location between tasks. These studies concluded that SM1 was primarily activated by proprioceptive reafferents, with negligible effects of cutaneous input. In our recent low-CMC study of the tongue, we concluded that low-CMC reflects proprioceptive afferents from the tongue to the primary somatosensory cortex (S1) during isometric tongue protrusion, since the MEG signal for low-CMC followed the EMG signal and the cortical sources of low-CMC originated in S1 [27].

In contrast with the consistent detection of low-CMC for the tongue, previous studies have not stably observed low-CMC for the fingers [1,18]. This finding may be explained by the different fiber composition of tongue muscles and limb muscles. The human

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