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Modulation of stimulus-induced 20-Hz activity for the tongue and hard palate during tongue movement in humans

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Abbreviations: ERD, event-related desynchronization; ERS, event-related synchronization; MEG, magnetoencephalography; SM1, primary sensorimotor cortex; TSE, temporal spectral evolution analysis.

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Highlights

- Magnetic 20-Hz event-related synchronization (ERS) was detected in response to tongue and hard palate stimulation at rest, but was inhibited by tongue movement.
- ERS was induced by oral stimulation, with or without proprioception, but was inhibited by tongue movement regardless of the stimulation or movement area.
- The results suggest that 20-Hz cortical coordination of the oral sensorimotor system is important for oral movements.

Abstract

Objective: Modulation of 20-Hz activity in the primary sensorimotor cortex (SM1) may be important for oral functions. Here, we show that 20-Hz event-related desynchronization/synchronization (20-Hz ERD/ERS) is modulated by sensory input and motor output in the oral region.

Methods: Magnetic 20-Hz activity was recorded following right-sided tongue stimulation during rest (Rest) and self-paced repetitive tongue movement (Move). To exclude proprioception effects, 20-Hz activity induced by right-sided hard palate stimulation was also recorded. The 20-Hz activity in the two conditions was compared via temporal spectral evolution analyses.

Results: 20-Hz ERD/ERS was detected over bilateral temporoparietal areas in the Rest condition for both regions. Moreover, 20-Hz ERS was significantly suppressed in the

Move condition for both regions.

Conclusions: Detection of 20-Hz ERD/ERS during the Rest condition for both regions suggests that the SM1 functional state may be modulated by oral stimulation, with or without proprioceptive effects. Moreover, the suppression of 20-Hz ERS for the hard palate during the Move condition suggests that the stimulation-induced functional state of SM1 may have been modulated by the movement, even though the movement and stimulation areas were different.

Significance: Sensorimotor function of the general oral region may be finely coordinated through 20-Hz cortical oscillation.

Keywords: Magnetoencephalography; MEG; Oral function; Event-related desynchronization; Event-related synchronization; Temporal spectral evolution

1. Introduction

The primary sensorimotor cortex (SM1) of relaxed humans shows oscillatory activity at around 20 Hz and 10 Hz. The 20-Hz and 10-Hz oscillations reportedly originate in the precentral cortex and postcentral cortex, respectively, as determined using invasive electroencephalography recordings (iEEG) (Arroyo et al., 1993; Toro et al., 1994) and magnetoencephalography (MEG) recordings (Hari and Salmelin, 1997; Salmelin et al., 1995). However, other iEEG studies have reported that the 20-Hz and 10-Hz oscillations originate from both the pre- and postcentral cortices (Crone et al., 1998; Ohara et al., 2000), thus concluding that such specific cortical generators do not exist.

It has been previously reported that event-related desynchronization/synchronization (ERD/ERS) around 20 Hz is induced by median nerve stimulation, and that the 20-Hz ERD/ERS is highly reproducible (Hari and Salmelin, 1997). MEG studies have shown that the 20-Hz ERS is completely suppressed when subjects execute actual hand movements (Salmelin and Hari, 1994a) and partially suppressed when subjects imagine themselves performing hand movements (Schnizler et al., 1997). In one prominent view, the 20-Hz ERS induced by peripheral nerve stimulation reflects an aspect of the “idling” state of SM1, which would allow the system to start more rapidly compared to using a “cold” start (Hari and Salmelin, 1997; Kuhlman, 1978; Pfurtscheller et al., 1997). Several recent studies promote an alternative view in which the 20-Hz ERS indicates an SM1 stabilization process (Caetano et al., 2007), whereby SM1 is shielded from external input and activation by new movements (Gilbertson et al., 2005).

Most studies on 20-Hz activity have focused on regions of the upper or lower extremities. However, a few previous studies have reported the presence of 20-Hz activity in association with oral movement using iEEG recordings (Crone et al., 1998; Miller et al., 2007). For instance, Crone et al. (1998) reported that compared to ERD at 8–13 Hz, ERD at 15–25 Hz showed more discrete somatotopic organization between different body parts (the tongue, arm, and foot) as assessed by a task comprised of visually cued isometric contractions of different body parts. Miller et al. (2007) reported that the spatial distribution of the cortical activity at 8–23 Hz was associated with tongue and hand movements. Furthermore, the activation at 8–23 Hz originated from a broader area than did the activation in the high frequency band at 76–100 Hz. Moreover, the generation of the activity at 8–23 Hz revealed a somatotopic representation between the hand and tongue. Somatotopic organization of 20-Hz activity has also been reported using non-invasive MEG recordings (Salmelin et al., 1995). The 20-Hz magnetic signal shows somatotopic organization for the toes, fingers, and mouth, but such specificity was not observed for the 10-Hz signal. As stated above, some studies reported 20-Hz activity in association with oral movement. However, little is known regarding the presence of 20-Hz activity following cutaneous stimulation of the oral region, or about the degree of stimulus-induced 20-Hz activity modulation during oral movement.

The tongue plays important roles in fine oral functions, such as mastication, speech, swallowing, and airway patency. The 20-Hz activity of SM1 may play an important role in sophisticated tongue movements, as a recent MEG study reported that the oscillatory cortical activity is coherent at 15–35 Hz with tongue muscle activity during isometric tongue protrusion (Maezawa et al., 2014a). Sensory input from the tongue and hard palate contains critical information for the execution of oral functions, as the tongue and hard palate contact each other constantly during mastication. However, the mechanism of peripheral sensory input is different between these two regions, specifically with regard to the presence or absence of fine motor function. This difference in the type of sensory input is advantageous for measuring 20-Hz activity using oral stimulation. Because the hard palate lacks muscle and joint receptors, “pure” cutaneous stimulation can be applied to the hard palate without interference from proprioception. In contrast, proprioceptive feedback effects from the tongue muscle can potentially occur when stimulating the tongue because the human tongue muscles are rich in muscle spindles.

Previous reports have shown that 20-Hz ERD/ERS can be detected by electrical stimulation of the median nerve (Ichikawa et al., 2007; Salenius et al., 1997b; Salmelin and Hari, 1994a, 1994b). However, because the intensity of the electrical stimulation was set to exceed the motor threshold in these studies, the effects of proprioceptive afferent input from the muscles or joints could not be excluded. Thus, because it remains unclear whether 20-Hz ERD/ERS was induced by the “pure” cutaneous stimulation without the effects of proprioception, it is important to assess the 20-Hz ERD/ERS evoked by stimulation of the hard palate and tongue, as cutaneous stimulation can be applied to the hard palate and tongue without and with the potential effects of proprioception, respectively.

The objective of this study was to investigate the modulation of 20-Hz activity related to oral sensorimotor function by using MEG to first identify whether 20-Hz ERD/ERS can be induced by stimulating the tongue and hard palate, and then examining how 20-Hz ERD/ERS is modulated by tongue and hard palate stimulation during tongue movement.

2. Methods

2.1. Subjects

The MEG recording experiments were conducted in 9 healthy right-handed subjects (6 males, 3 females; age, 19–35 years; mean age, 24.9 years). The study was performed in conformity with the Declaration of Helsinki and approved by the Ethical Committee of Dental Medicine of Hokkaido University.

2.2. Tasks

The experiment consisted of the following two conditions: (1) the Rest condition, during which the subjects rested and relaxed without moving; and (2) the Move condition, during which the subjects performed repetitive tongue movements at a self-paced rhythm of approximately 1 Hz. These tongue movements were performed with the subject's mouth slightly open and without the tongue touching the lips, teeth, or hard palate to the greatest possible extent. The subjects looked at a point on the front wall during all measurements. To monitor subjects' alertness during the recordings, the subjects were interviewed about their vigilance level before and after each recording session.

2.3. Stimulation

Stimulation was applied on the right side of the tongue and hard palate using an electrical stimulator (SEN-3401, Nihon Kohden, Tokyo, Japan) in each condition (Rest and Move). Thus, the experiment consisted of the following four sessions: (1) tongue stimulation during the Rest condition, (2) tongue stimulation during the Move condition, (3) hard palate stimulation during the Rest condition, and (4) hard palate stimulation during the Move condition. Each session lasted approximately 4 min, with short intervening pauses, and each session was performed twice. The order of these sessions was counterbalanced across subjects. A pair of pin electrodes (400-μm diameter) with an inter-electrode distance of 3 mm was used for stimulation because these electrodes can safely administer a low-intensity stimulus to a small oral region, which is advantageous because it prevents oral muscle twitches following electrical stimulation (Maezawa et al., 2008, 2011, 2014b). The electrodes were affixed using adhesive tape. Tongue stimulation was applied 1 cm from the edge of the tongue, 3–4 cm from the tongue tip. For the hard palate, stimulation was applied to the mucosa around the greater palatine foramen (Maezawa et al., 2014c). Using self-reports, we confirmed that subjects felt electrical sensation only at the stimulation point throughout the recording in each condition (Rest and Move). The intensity was set to 2.5 to 3 times the sensory threshold for each stimulation site. The intensity for the tongue was below the motor threshold in all subjects. The stimulus consisted of square, biphasic, constant-current electric pulses (0.5 ms for 1 phase) applied once every 2.0–2.5 s. Stimulation was applied at least 90 times in each session. Group-averaged data from the two sessions were used for later analysis.

2.4. Recording

MEG signals were recorded with a helmet-shaped, 306-channel, whole-head neuromagnetometer (Vectorview; Elekta Neuromag, Finland), which was equipped with 102 sensor units consisting of two planar gradiometers and one magnetometer. In this study, data recorded from 204 planar gradiometers were used for analyses because they can detect the largest signal just above the corresponding generator source (Hämäläinen et al., 1993). The recording passband was 0.1–330 Hz and the sampling rate was 997 Hz, and the recording was stored for off-line analysis.

Somatosensory evoked magnetic fields (SEFs) were also recorded using an on-line averaging system. To check that the target region (tongue and hard palate) was stimulated successfully in each condition, we confirmed that SEFs were clearly shown over both hemispheres throughout the recording.

2.5. Data analysis

To minimize the effects of artifacts during the recording, the raw data were spatially filtered off-line using the temporal extension of signal space separation method (Taulu and Simola, 2006 and Taulu and Hari, 2009) with the MaxFilter software (version 2.2.10, Elekta Neuromag, Finland).

ERD/ERS was defined as a time-locked decrease/increase in the amplitude of the rhythmic cortical activity in response to electrical stimulation. ERD/ERS was evaluated by temporal spectral evolution (TSE) analysis (Salmelin and Hari, 1994a, 1994b). The continuous MEG signals were filtered through passbands of 18–23 Hz and then rectified (Ichikawa et al., 2007; Kinai et al., 2009; Tominaga et al., 2009). MEG epochs from 0.2 s before to 2.0 s after the onset of the stimulus were collected. Each epoch was inspected visually, and all epochs coinciding with significant blinks or eye movements were excluded from the data analysis. The rectified MEG signals within the selected epochs were averaged with respect to the onset of the stimulus and smoothed with a 10-Hz low-pass filter.

To quantify the ERD/ERS in each condition for both regions (tongue and hard palate), the data from the most reactive sensor with the largest amplitude difference between the maximum suppression and maximum enhancement in each hemisphere were used to quantify the modulation of the oscillatory activity. The latency of the ERD/ERS was defined as the point when the maximum suppression/enhancement value was reached within 100 to 1500 ms after stimulation onset. To analyze the ERD/ERS amplitude, the mean value acquired from 10 ms before to 10 ms after the time of maximal suppression/enhancement was used (Enatsu et al., 2014). Moreover, to assess the percent decrease/increase in the ERD/ERS amplitude from baseline, the mean amplitude of the ERD/ERS before and after the maximal suppression/enhancement was evaluated relative to the baseline value. The 200-ms period prior to stimulus onset (from −200 to 0 ms) was used as the baseline period. Responses with greater than a 5% decrease/increase from the baseline during the Rest condition were accepted for further analysis (Enatsu et al., 2014).

Data are expressed as the mean ± the standard error of the mean (SEM). For statistical analysis, the percent change in ERD/ERS was compared using a two-way repeated measures analysis of variance (ANOVA) with the within-subjects factors of condition (Rest vs. Move) and stimulation region (tongue vs. hard palate). Post-hoc comparisons were performed using paired *t*-tests with Bonferroni correction. Significance was set at $p < 0.05$.

3. Results

One subject (subject 9; male, age 19) was excluded from the TSE analysis because of an absence of reactive 20-Hz oscillations. The present results, therefore, are based on 8 subjects (5 males, 3 females; age range, 21–35 years; mean age, 25.6 years).

3.1. Tongue stimulation

Fig. 1A1 shows spontaneous MEG activity bandpass filtered through 18–23 Hz from a representative channel over the contralateral (left) temporoparietal area during the Rest condition following stimulation of the right side of the tongue in a single subject (subject 5). Amplitude fluctuation of the 20-Hz rhythmic activity was observed. The bursts of 20-Hz activity observed during the Rest condition were almost completely suppressed during the Move condition (Fig. 1A2).

Using TSE analyses, the 20-Hz ERD/ERS evoked by electrical tongue stimulation was evaluated. During the Rest condition, prominent suppression and increases in the TSE waveform were observed over the bilateral temporoparietal areas in a representative subject (subject 7) (Fig. 2A). 20-Hz ERD was detected at 354 ms after stimulation onset over the contralateral hemisphere with a 14.1% suppression from the baseline period, and at 431 ms over the ipsilateral hemisphere with a 16.3% suppression. Additionally, in the contralateral (left) hemisphere, 20-Hz ERS was detected at 1052 ms after stimulation onset with an 18.0% increase from the baseline period (Fig 2B). In the ipsilateral (right) hemisphere, 20-Hz activity was observed at 1028 ms after stimulation onset with a 23.1% increase from the baseline period (Fig. 2C).

The source locations of ERS were located around the lower part of the pre- and post-central sulcus in a representative subject (subject 7), suggesting that the 20-Hz ERS for the tongue originated from the sensorimotor cortex (Supplementary Fig. S1).

20-Hz ERD was detected at 346.9 ± 55.7 ms (range: 180–540 ms) over the contralateral (left) hemisphere in 7 subjects, and at 377.8 ± 69.1 ms (range: 225–542 ms) over the ipsilateral (right) hemisphere in 4 subjects during the Rest condition (Fig. 3).

During the Rest condition, 20-Hz ERS was detected over the contralateral (left) hemisphere in 8 subjects, and over the ipsilateral (right) hemisphere in 6 subjects, based on the criterion of showing a 5% increase from the baseline period (Fig. 3). The mean latencies of the 20-Hz ERS peaks were observed at 842.3 ± 64.2 ms (range: 661–1142 ms) and at 990.8 ± 59.2 ms (range: 814–1242 ms) over the contralateral and ipsilateral hemispheres, respectively, after tongue stimulation. The time course of the 20-Hz ERS during the Rest condition was consistent with the 20-Hz ERS evoked in previous MEG studies by the stimulation of other human body parts such as the upper limbs (Hari et al., 1998; Schnitzler et al., 1997; Tominaga et al., 2009), fingers (Enatsu et al., 2014), and lower limbs (Kinai et al., 2009).

3.2. Hard palate stimulation

One subject (subject 8; female, age 24) was excluded from the MEG recordings during hard palate stimulation because it was difficult to stimulate the hard palate as a result of palatine torus. Therefore, the results for the hard palate are based on 7 subjects (5 males, 2 females; age range, 21–35 years, mean age, 25.9 years).

Fig. 1B shows spontaneous 20-Hz MEG activity above the contralateral (left) hemisphere during the Rest and Move conditions in a single subject (subject 5). Obvious bursts of 20-Hz activity were observed during the Rest condition, but were suppressed during the Move condition.

20-Hz ERD was detected at 330.8.6 ± 32.4 ms (range: 258–420 ms) over the contralateral (left) hemisphere in 5 subjects, and at 311.5 ± 93.2 ms (range: 162–580 ms) over the ipsilateral (right) hemisphere in 4 subjects during the Rest condition (Fig. 3).

Moreover, in the Rest condition, 20-Hz ERS was detected over the contralateral (left) hemisphere in 7 subjects and over the ipsilateral (right) hemisphere in 7 subjects, based on the criterion of showing a 5% increase from the baseline period (Fig. 4). Prominent ERS peaks were observed at 779.0 ± 92.1 ms (range: 520–1187 ms) and at 803.7 ± 140.9 ms (range: 421–1334 ms) over the contralateral and ipsilateral hemispheres, respectively, after hard palate stimulation.

3.3. Percent change

3.3.1. 20-Hz ERD

In the Rest condition, the mean percent decrease in 20-Hz ERD for the tongue were 12.1 ± 0.8% (range: 9.2–15.4%) and 13.6 ± 1.0% (range: 11.6–16.3%) over the contralateral and ipsilateral hemispheres, respectively. The mean percent decrease in 20-Hz ERD for the hard palate were 12.1 ± 1.4% (range: 9.1–16.9%) and 10.6 ± 1.1% (range: 8.7–13.4%) over the contralateral and ipsilateral hemispheres, respectively.

In the Move condition, the mean percent decrease in ERD for the tongue were 4.3 ± 1.0% (range: 0.9–8.7%) and 5.2 ± 0.5% (range: 3.8–6.0%) over the contralateral and ipsilateral hemispheres, respectively. The mean percent decrease in the ERD for the hard palate were 6.1 ± 0.9% (range: 4.4–9.7%) and 2.7 ± 1.3% (range: 0–5.3%) over the contralateral and ipsilateral hemispheres, respectively (Fig. 5A).

The percent change in ERD was excluded from the statistical analysis because of the small sample size.

3.3.2. 20-Hz ERS

The mean percent increases in 20-Hz ERS for the tongue were 15.7 ± 2.1%

(range: 6.7–24.6%) and 16.9 ± 2.7% (range: 6.6–23.1%) over the contralateral and ipsilateral hemispheres, respectively (Fig. 5). The mean percent increases in 20-Hz ERS for the hard palate were 12.1 ± 1.5% (range: 6.9–16.4%) and 13.3 ± 1.4% (range: 7.9–17.2%) over the contralateral and ipsilateral hemispheres, respectively (Fig. 5).

In the Move condition, the mean percent increases in ERS for the tongue were 5.4 ± 1.0% (range: 0–9.3%) and 6.7 ± 1.0% (range: 3.4–9.1%) over the contralateral and ipsilateral hemispheres, respectively (Fig. 5). The mean percent increases in ERS for the hard palate were 5.8 ± 1.1% (range: 1.9–9.0%) and 5.6 ± 1.8% (range: -2.7–12.4%) over the contralateral and ipsilateral hemispheres, respectively (Fig. 5).

Statistical analysis of the percent change in ERS for the contralateral hemisphere showed a significant main effect of condition (Rest vs. Move) ($p = 0.001$), but no significant main effect of stimulation region (tongue vs. hard palate) ($p = 0.500$) or a significant interaction ($p = 0.240$). Statistical analysis of the percent change in ERS for the ipsilateral hemisphere showed a significant main effect of condition (Rest vs. Move) ($p = 0.011$), but no significant main effect of stimulation region (tongue vs. hard palate) ($p = 0.395$) or a significant interaction ($p = 0.982$). The paired *t*-tests with Bonferroni correction revealed that the percent changes in ERS for the Rest condition were significantly larger than the changes in ERS for the Move condition for each stimulation region in both the contralateral (tongue, $p = 0.004$; hard palate, $p = 0.002$) and ipsilateral (tongue, $p = 0.030$; hard palate, $p = 0.030$) hemispheres.

4. Discussion

The current study demonstrated the presence of 20-Hz ERD/ERS over both hemispheres following tongue and hard palate stimulation. Moreover, the 20-Hz ERS was significantly suppressed during tongue movement for both regions. These results suggest that the functional state of SM1 may be modulated by cutaneous stimulation of the oral region, with or without the effects of proprioception. Our findings also suggest that the functional state of SM1 induced by stimulation may be modulated by the movement even when the stimulation region is different from the movement region in the oral area.

4.1. Rest condition

We showed that the 20-Hz ERD/ERS induced by oral stimulation is similar to the 20-Hz ERD/ERS generated by limb stimulation (Kinai et al., 2009; Salmelin and Hari, 1994a, 1994b). The functional meaning of this 20-Hz activity is still unknown. Currently, the leading hypothesis is that 20-Hz activity represents the “active inhibition” state of SM1 when body parts are at rest, and that 20-Hz activity may indicate a stabilization process of SM1 (van Wijk et al., 2012). Given the hypothesis, oral stimulation, similarly to limb stimulation, may modulate the functional state of SM1.

In a recent ERD/ERS study using MEG, the effects of proprioceptive sensation from the muscle tendon and finger joint were minimalized by applying electrical stimulation to the digital nerve (Enatsu et al., 2014). However, as the fingers have muscles and joints that enable fine motor function, the stimulation may have activated the proprioceptive nerves of the fingers to some extent, and the effects of such activation on 20-Hz activity cannot be excluded. In fact, several previous studies suggested that proprioception affects oscillatory activity, as passive movement induced somatosensory-evoked magnetic fields (Xiang et al., 1997) or somatosensory-evoked potentials (Mima et al., 1996) and modulated the oscillatory activity in SM1 (Alegre et al., 2002; Cassim et al., 2001). Until now, it remained unclear whether ERD/ERS could be induced by “pure” cutaneous stimulation without proprioception. The present study sought to clarify this point by applying electrical stimulation to the hard palate region, as the hard palate does not have any motor function and cutaneous stimulation can be applied without the effects of proprioception from the muscles or joints. Electrical stimulation of the hard palate was considered “pure” cutaneous input, in contrast to tongue stimulation, which was not “pure” because the possibility of proprioceptive contamination from the tongue muscle could not be excluded. Because the source location of the ERS for the tongue during the Rest condition was located in SM1 in a representative subject, the functional state of SM1 was likely modulated by cutaneous stimulation of the oral region, with or without the effects of proprioception. Given that stimulation of the hard palate, a region without proprioception, induced 20-Hz activity, this indicates that the presence of proprioceptive feedback is not required for producing the 20-Hz activity.

4.2. Move condition

Previous MEG studies have shown that the 20-Hz ERS induced by median nerve stimulation is almost completely suppressed when executing finger movements (Salmelin and Hari, 1994a) and partially suppressed during motor imagery (Schnitzler et al., 1997). These studies indicate that the suppression of stimulus-induced 20-Hz ERS reflects the neural activation of SM1 (Hari et al., 1998; Schnitzler et al., 1997). However, most brain-imaging studies have reported activity related to the upper or lower extremities, whereas few studies have focused on oral motor function. In the present study, we demonstrated that the 20-Hz activity induced by oral stimulation is suppressed during tongue movement, which is similar to effects previously observed in the extremities. Recent studies reported that boosting the 20-Hz activity using transcranial alternating-current stimulation impaired the execution of new movements, suggesting that 20-Hz activity may be mechanistically important for motor behaviors (Joundi et al., 2012; Pogosyan et al., 2009). Collectively, these studies imply that the modulation of oral 20-Hz activity may underlie the execution of precise oral movements.

The result showing that stimulus-induced 20-Hz activity was suppressed for the hard palate during tongue movement is particularly important because the movement region was different from the region being stimulated. Regarding the hypothesis that 20-Hz ERS represents the inhibition state of SM1, this result suggests that the functional state of SM1 induced by cutaneous stimulation might be modulated by movement, even if the stimulation and movement regions are different in the oral area. As the tongue and hard palate contact each other constantly during mastication, sensory feedback from these regions may be critical for fine tongue movements. Such dynamic modulation of 20-Hz oscillation by hard palate stimulation during tongue movement may result from a close interrelationship between the neuronal circuits related to the sensorimotor systems for the tongue and hard palate.

Previous studies reported that the tongue region in the primary motor cortex may overlap neighboring oral regions in this area, such as the regions for the lips, mandible, and soft palate, as determined using MEG (Maezawa et al., 2014) or functional magnetic resonance imaging (Martin et al., 1997; Meier et al., 2008). Therefore, simple tongue movements may require cooperative mobilization between these general oral areas. Given these findings, the observed modulation of oral 20-Hz activity during tongue movement suggests dynamic oscillatory coordination of the sensorimotor systems of the general oral area, which may contribute to sophisticated oral functions. In rehabilitation therapy, the modulation of 20-Hz activity by sensory input, motor output, and motor imagery is reportedly beneficial for improving functional impairments in the extremities (Ichikawa et al., 2007; Tominaga et al., 2009). Because impairments in oral functions, such as dysphagia or speech disorders, can cause a severe decrease in patients’ quality of life, modulating the 20-Hz activity for the oral region may also be useful for improving oral dysfunction.

4.3. Limitations

This study has three limitations. First, the observed suppression of 20-Hz ERS for both the tongue and hard palate during tongue movement led us to conclude that the neuronal circuits for the sensorimotor functions of the tongue and hard palate may be closely related. However, since we did not perform a negative control study to show that the 20-Hz ERS was not modulated by the stimulation of a body part unrelated body to oral function, such as the upper face, during tongue movement, we cannot fully establish the relevance of hard palate sensation to tongue movement. This point is a potential weakness of the study.

The second limitation is related to head movement during recording. To quantify the ERD/ERS in each condition, we analyzed the most reactive sensor. However, as the position of the head may vary in the helmet, especially during the Move condition, the maximum signal may have shifted from one sensor to another; thus, we cannot rule out the potential effects of head movement on the recording. Applying continuous head position compensation with the Maxfilter software may be useful for reducing the head movement effects during recording in future studies (Taulu et al., 2005).

Third, we could not determine the somatotopic organization for the 20-Hz ERD/ERS between the oral region and other body parts. Additional research is needed to explore the precise source locations of oral ERD/ERS as compared with the source locations of limb ERD/ERS.

5. Conclusions

In conclusion, oscillatory cortical activity was modulated by sensory input and motor output in the oral region, similar to the modulation observed following limb stimulation. The detection of stimulus-induced 20-Hz activity for the tongue and hard palate indicates that cutaneous stimulation, regardless of proprioceptive input, may modulate the functional state of SM1. Moreover, the suppression of stimulus-induced 20-Hz activity observed for both regions during tongue movement suggests that the stimulus-induced functional state of SM1 may be modulated by movement, even when the stimulated region is different from the oral region undergoing movement. This finding suggests that the neuronal circuits involved in the sensorimotor function of the tongue and hard palate may be closely related. Sensorimotor function of the general oral region may be finely coordinated through 20-Hz cortical oscillation.

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Figure legends

Figure 1. Representative 20-Hz activity from a channel over the contralateral (left) sensorimotor cortex following stimulation of the right side of the tongue and hard palate in subject 5. First, we applied the temporal extension of signal space separation to the raw data signals, and then we bandpass filtered the raw data through 18–23 Hz. Vertical dashed lines indicate the onset of electrical stimulation. Bursts of 20-Hz activity were detected for either the tongue (A1) or hard palate (B1) during the Rest condition, but were suppressed in the Move condition for both regions (A2, B2). Note that we could successfully remove the stimulation artifacts with low electrical stimulation intensity by using pin electrodes. Rest, Rest condition; Move, Movement condition.

Figure 2. The whole-head magnetic waveforms of event-related desynchronization/synchronization (ERD/ERS) around 20-Hz following stimulation of the right side of the tongue in a representative subject (subject 7) and quantified with the temporal spectral evolution (TSE) method. A. The top view of the TSE recorded by the planar 204-channel recording shows clear ERD and ERS over the bilateral parietotemporal areas. Each trace goes from 200 ms before to 1500 ms after stimulation onset. As shown in the expanded waveforms (B, C), ERD and ERS were detected over the contralateral and ipsilateral hemispheres (indicated by outlined arrowheads [ERD] and filled arrowheads [ERS]) based on the percent change criterion of the maximum suppression/enhancement from the baseline period (see Section 2.5. in the Methods for details).

Figure 3. Changes in event-related desynchronization/synchronization (ERD/ERS)

around 20-Hz between the Rest and Move conditions for the tongue over both hemispheres in all 8 subjects. The 20-Hz ERD/ERS curves were obtained from the most reactive channel over each hemisphere in each condition (see Section 2.5. in the Methods for details). The solid and dashed lines indicate the waveforms obtained from the Rest and Move conditions, respectively. Each trace was obtained from 200 ms before to 1500 ms after stimulation onset. ERD/ERS (indicated by outlined arrowheads [ERD] and filled arrowheads [ERS]) were assessed by the percent change criterion based on the mean amplitude of the baseline period in the Rest condition (see Section 2.5 in the Methods for details). ERS was constantly detected over both hemispheres in the Rest condition except in two subjects where responses were not detected over the ipsilateral hemispheres (subjects 6 and 8). ERS was obviously suppressed in the Move condition. Contra., Contralateral hemisphere; Ipsi., Ipsilateral hemisphere; Rest, Rest condition; Move, Movement condition; Subject, Subject number.

Figure 4. Changes in event-related desynchronization/synchronization (ERD/ERS) around 20-Hz between the Rest and Move conditions for the hard palate over both hemispheres in all 7 subjects. Waveforms were obtained from the most reactive channel over each hemisphere in each condition. The solid and dashed lines indicate the curves obtained from the Rest and Move conditions, respectively. Each trace was obtained from 200 ms before to 1500 ms after stimulation onset. ERD/ERS (indicated by outlined arrowheads [ERD] and filled arrowheads [ERS]) were assessed by the percent change criterion based on the mean amplitude of the baseline period in the Rest condition. Note that ERS was constantly detected over both hemispheres in the Rest condition, but was suppressed in the Move condition. Contra., Contralateral hemisphere;

Ipsi., Ipsilateral hemisphere; Rest, Rest condition; Move, Movement condition; Subject, Subject number.

Figure 5. Mean ± standard error of the mean values of the percent change in the event-related synchronization (ERS) levels across subjects. The percent increase in the ERS level was significantly smaller in the Move condition than in the Rest condition for the tongue and hard palate in both hemispheres (each column: n = 8 [Contra., Tongue], n = 6 [Contra., Hard palate], n = 7 [Ipsi., Tongue and Hard palate]). Asterisks indicate statistically significant differences ($p < 0.05$). Contra., Contralateral hemisphere; Ipsi., Ipsilateral hemisphere; Rest, Rest condition; Move, Movement condition; NS, Not significant.

Figure1

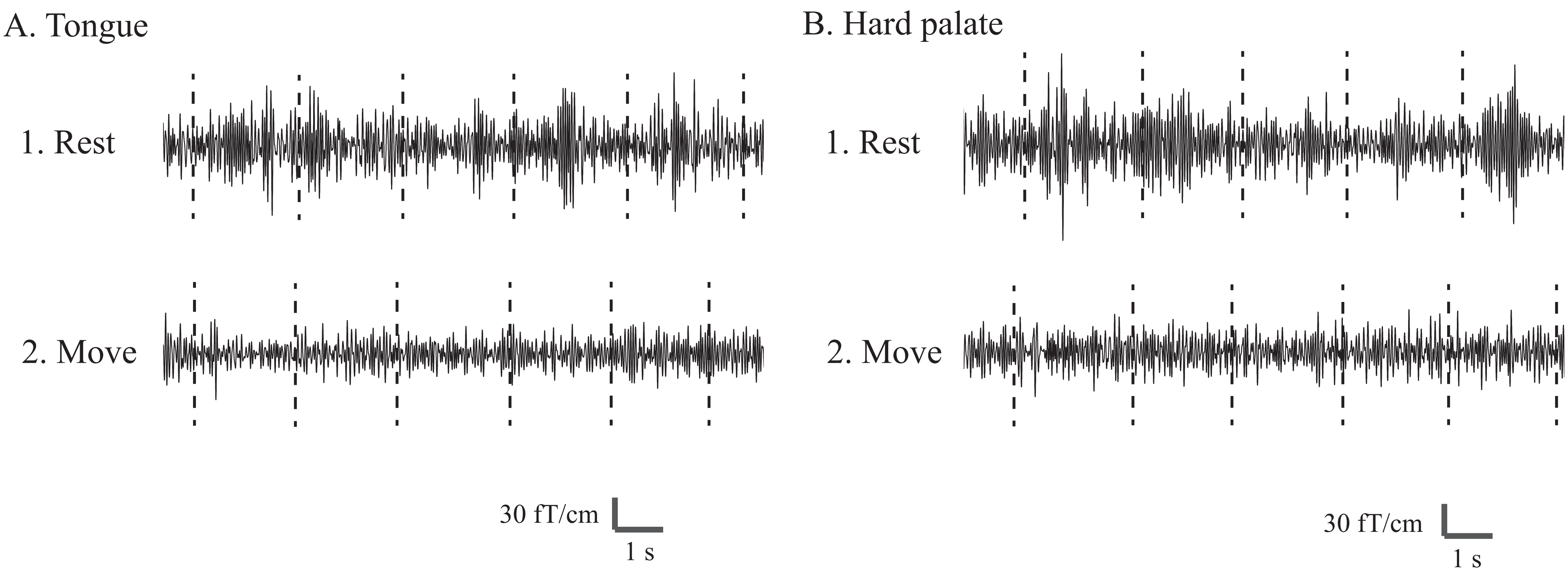

A. Tongue
B. Hard palate
1. Rest
2. Move
1. Rest
2. Move
30 fT/cm
1 s
30 fT/cm
1 s

Figure2

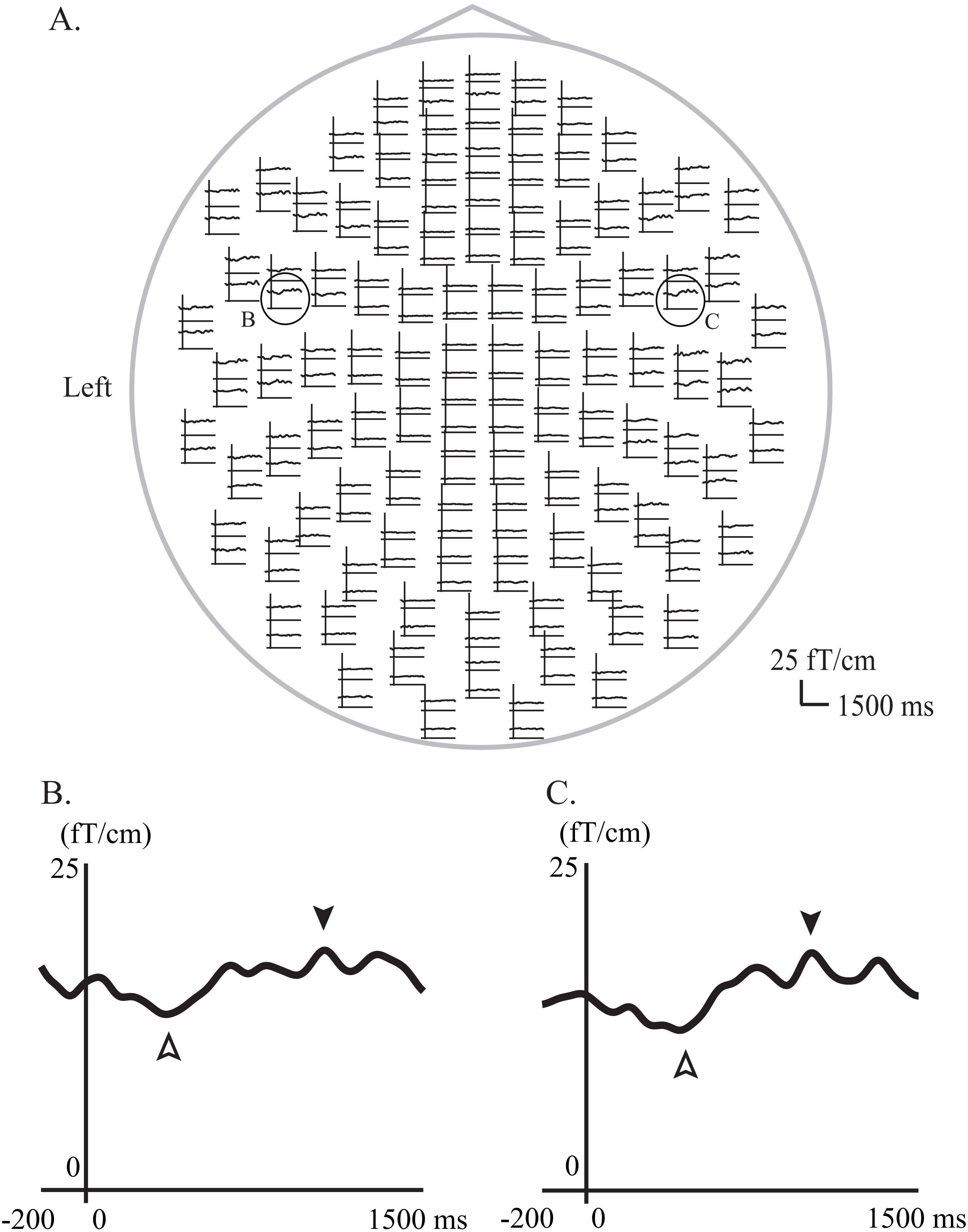

A.
Left
B
C
25 fT/cm
1500 ms
B.
(fT/cm)
25
0
-200
0
1500 ms
C.
(fT/cm)
25
0
-200
0
1500 ms

Figure3

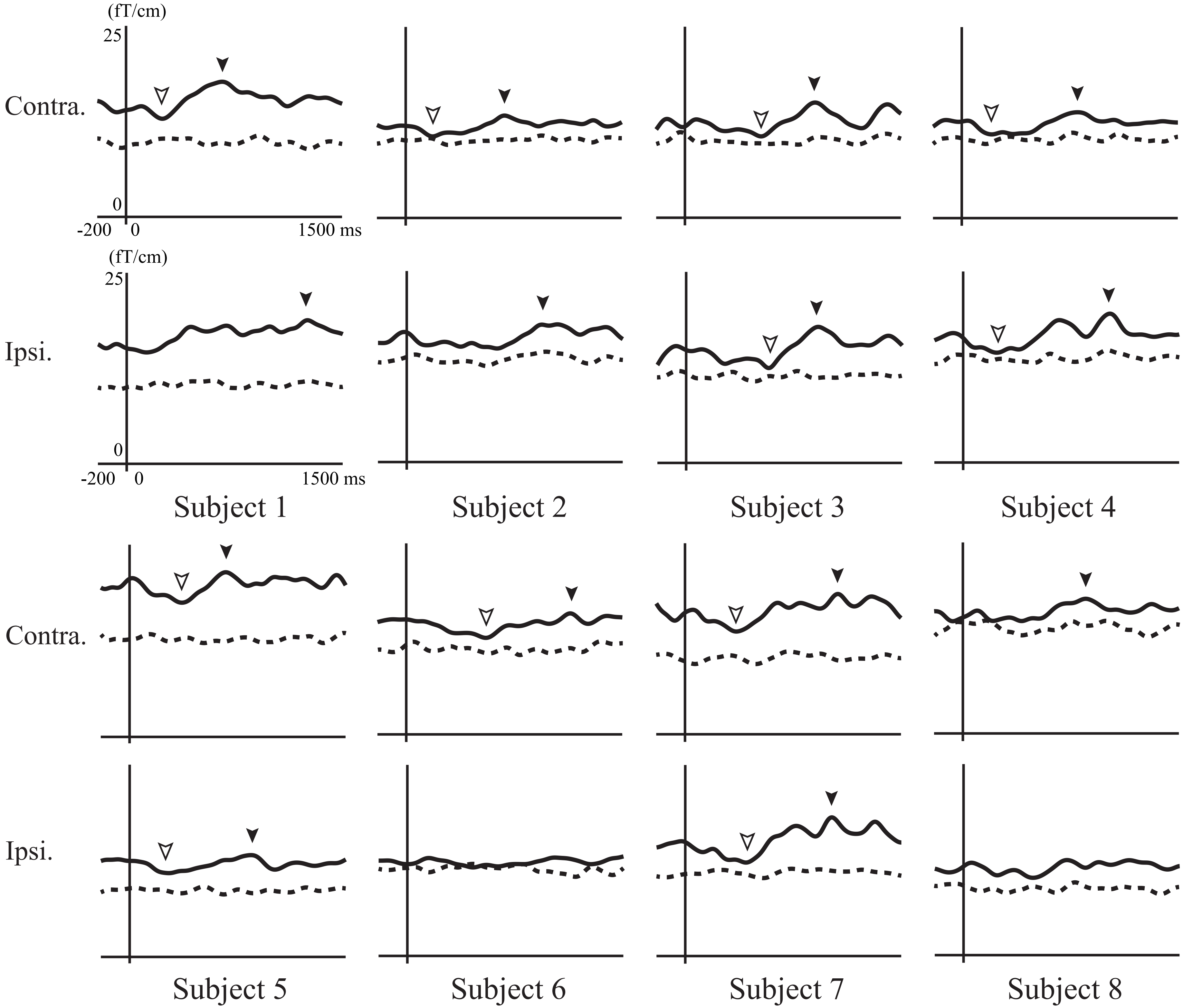

(fT/cm)
25
0
-200
0
1500 ms
Contra.
Ipsi.
Subject 1
Subject 2
Subject 3
Subject 4
Subject 5
Subject 6
Subject 7
Subject 8

Figure4

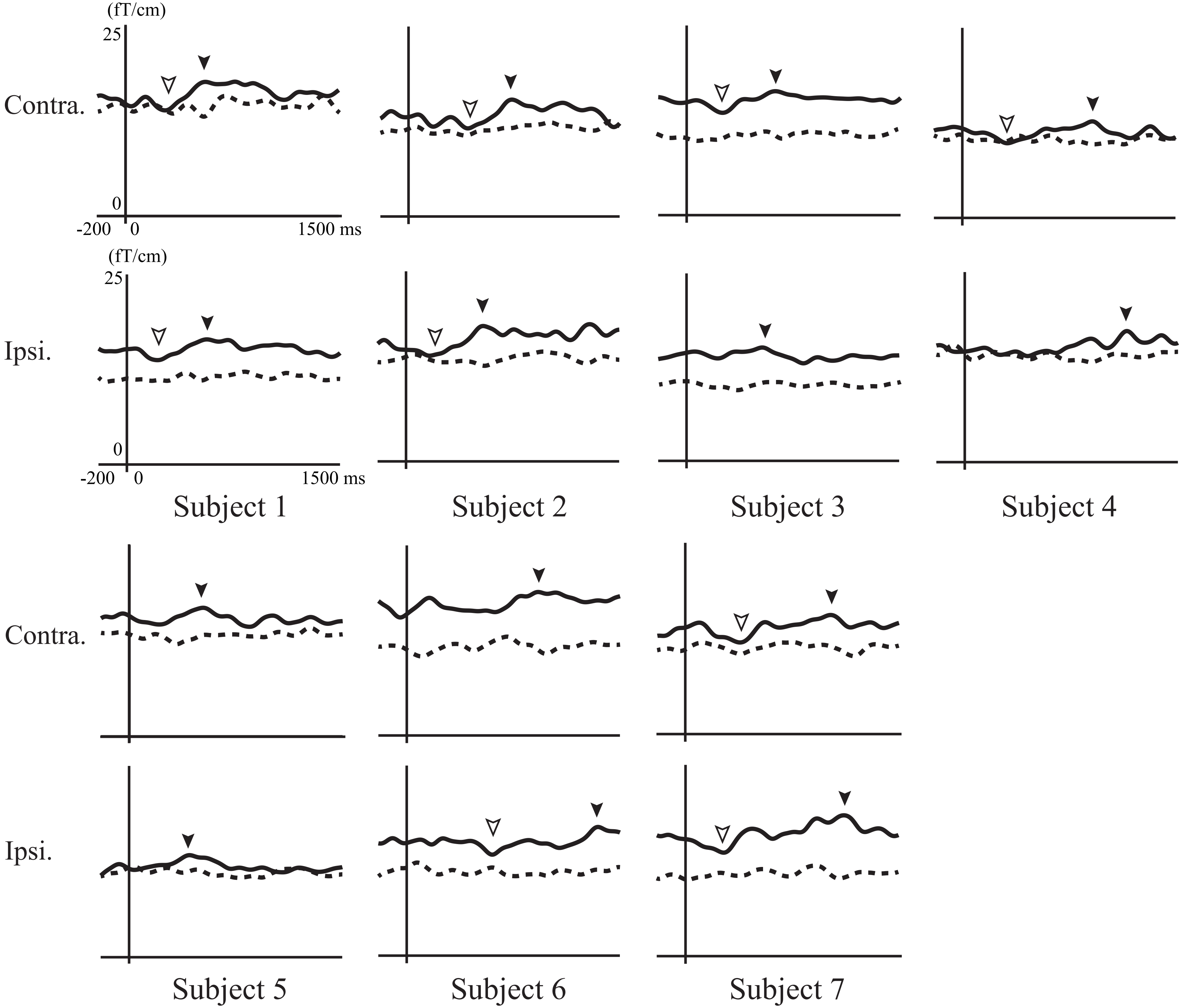
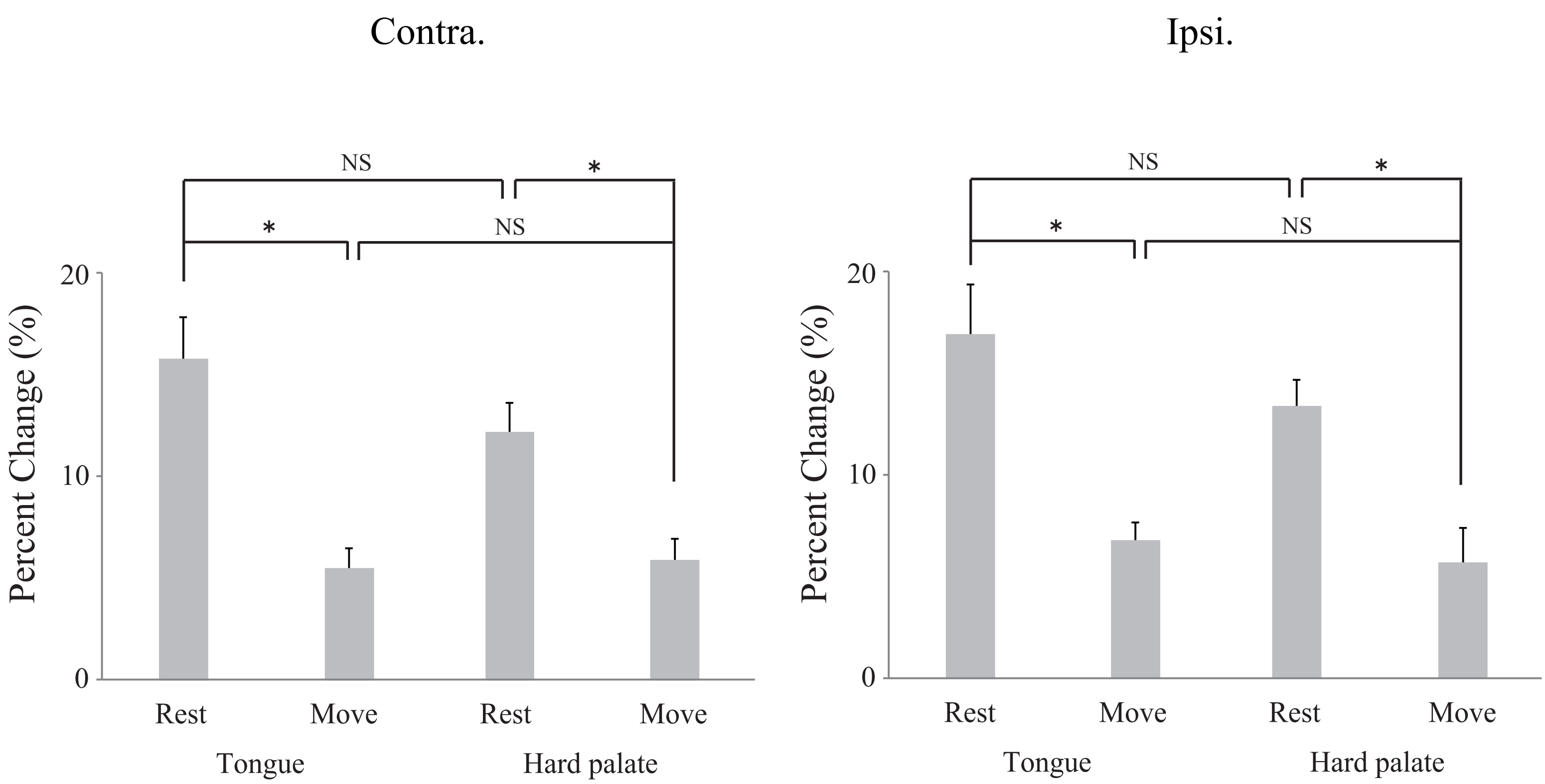

(fT/cm)
25
0
-200
0
1500 ms
Contra.
Ipsi.
Subject 1
Subject 2
Subject 3
Subject 4
Subject 5
Subject 6
Subject 7

Figure5



Contra.
Ipsi.
NS
*
NS
*
Percent Change (%)
20
10
0
Rest
Move
Rest
Move
Tongue
Hard palate