Direction-specific cortical response immediately after moving tactile stimuli in female humans

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Summary

This study looked for a direction-specific cortical response immediately after application of moving tactile stimuli in healthy female humans. Four pairs of stimulus electrodes were placed over the left index finger pulp on the distal-proximal axis. Four times, once in every 40 ms interval, an electrical stimulus to the finger pulp was delivered through one of the four pairs of electrodes; each time the stimulus site changed in order to induce a sensation of tactile motion. The slope of the electroencephalographic trace, as recorded from electrodes placed over the CP, P4 and right hMT+/V5 in the period 150-200 ms after the onset of stimuli delivered in sequence from the distal to proximal site, was significantly different from that after stimuli delivered in sequence from the proximal to distal site. The cortical response immediately after the proximally-directed moving tactile stimuli was different from that after the distally-directed moving tactile stimuli in the hemisphere contralateral to the stimulus side.

KEY WORDS: cortical response, electroencephalography, hMT+/V5, moving tactile stimuli.

Introduction

When a human manipulates an object, a sensation of tactile motion is induced allowing the subject to perceive the characteristics of the object. Investigations have been carried out to elucidate the cortical processing underlying perception of moving tactile stimuli (Pei and Bensmaia, 2014). Five recent studies investigated cortical activity during application of moving tactile stimuli in humans (Bremmer et al., 2001; Hagen et al., 2002; Summers et al., 2009; Wacker et al., 2011; van Kemenade et al., 2014). In those studies, moving tactile stimuli induced cortical activity in the primary sensory cortex (SI), secondary sensory cortex (SII), posterior parietal cortex (PPC) and hMT+/V5. The hMT+/V5, in particular, has been suggested to be the site where motion processing occurs, regardless of the sensory modality involved (Sack et al., 2006; Matteau et al., 2010). Thus, the significant activity in hMT+/V5 during moving tactile stimuli observed in four out of the five recent studies may reflect motion processing (Hagen et al., 2002; Summers et al., 2009; Wacker et al., 2011; van Kemenade et al., 2014).

Such cortical activity, induced by moving tactile stimuli, may depend on the direction of these stimuli. Transcranial magnetic stimulation (TMS) over the SI and hMT+/V5 significantly reduced the ability to discriminate the direction of moving tactile stimuli, but TMS over the PPC did not (Amemiya et al., 2017). The SII, anterior insula, and dorsolateral prefrontal cortex contralateral to the stimulus side were found to be activated when discriminating the direction of skin pull stimulations (Lundblad et al., 2010). However, these findings do not constitute a demonstration of direction-specific cortical activity in response to moving tactile stimuli; rather, they indicate the site of cognitive processing for discriminating the direction of these stimuli.

The SI is directionally sensitive in monkeys (Ruiz et al., 1995). In humans, the activity of the SI and SII has been shown to depend on the direction of moving tactile stimuli, but this directional sensitivity has not been shown in hMT+/V5 (Wacker et al., 2011; van Kemenade et al., 2014). In these two studies in humans, fMRI was recorded during the task. According to somatosensory evoked potential (SEP) and event related potential findings (Valeriani et al., 2001), the cortical processing of the somatosensory stimulation ends 300 ms after the stimulation. Thus, the direction-specific cortical activity in the hMT+/V5 area may be observable by examining the electroencephalographic (EEG) response in the period 0-300 ms after the moving tactile stimulus.

The present study investigated direction-specific EEG response immediately after moving tactile stimuli in healthy female humans. Once in every 40 ms interval, an electrical stimulus was delivered to one of the four pairs of electrodes on the index finger pulp, and the stimulus site changed with each stimulus in order to induce a sensation of tactile motion. In our preliminary experiment, reproducible EEG responses were not observed during and immediately after the moving tactile stimuli. Thus, instead of studying peak responses, we estimated the slope of the EEG trace immediately after completion of the moving tactile stimulus. We hypothesized that the EEG slopes recorded from the electrodes over the hMT+/V5 would depend on the direction of the moving tactile stimuli. Somatosensory impairment is common in patients after stroke (Kim and Choi-Kwon, 1996; Carey and Matyas, 2011). However, no investigations of tactile motion sensation have been performed in these patients. If a direc-
tion-specific EEG response immediately after moving tactile stimuli were found to be observable, it could be a useful measure for evaluation of tactile motion sensation in patients with neurological diseases such as stroke. Moreover, measurement of this EEG response could be used in biofeedback training to promote recovery of tactile motion sensation in patients with tactile sensory disturbances.

Materials and methods

Participants

The participants were 10 healthy young females aged 19.4 ± 0.7 years. They had no history of neurological or orthopedic diseases. All participants were right handed according to Edinburgh Handedness Inventory (Oldfield, 1971). The experiment was conducted according to the Declaration of Helsinki and was approved by the ethics committee of Osaka Prefecture University.

Stimulus electrodes

Four pairs of stimulus electrodes, each 2 mm in diameter, were placed over the left index finger pulp (Fig. 1). The cathode was placed on the radial side of the finger pulp and the anode was placed at the site 5 mm ulnar to the cathode. The distance between each pair of the electrodes on the distal-proximal axis was 5 mm. Stimulus intensity was 1.1 times the perceptual threshold. The stimuli delivered were weak so that the participants did not feel pain.

EEG and EOG

Ag/AgCl recording electrodes were placed over the regions of interest; Fz, T3, T4, CP4, P3, and P4 in accordance with the 10-20 system, and over the hMT+/V5. The average locus of the hMT+/V5 is 3.6 cm anterior to and 5.1 cm lateral to the inion (Sack et al., 2006; Vetter et al., 2015; Amemiya et al., 2017). Thus, the electrode over the hMT+/V5 was placed over this locus. The hMT+/V5 was chosen because it has been found to be activated during moving tactile stimuli (Hagen et al., 2002; Summers et al., 2009; Wacker et al., 2011; van Kemenade et al., 2014). EEG response to the somatosensory stimulus at T3 and T4 represents the cortical response generated from the SII (Kany and Treede, 1997). CP4 has been considered to be the site over the SI (Brodie et al., 2014). EEG responses at CP4, T3 and T4 were measured because the SI and SII have been considered to be involved in tactile motion processing (Bremmer et al., 2001; Hagen et al., 2002; Summers et al., 2009; Wacker et al., 2011; van Kemenade et al., 2014), and direction-specific cortical activity during moving tactile stimuli has been observed at these sites (Wacker et al., 2011). CP3 was not measured, because previous studies found SI activity during moving tactile stimuli to be present only in the hemisphere contralateral to the stimulus side (Bodegård et al., 2000; Hagen et al., 2002; Summers et al., 2009; Lundblad et al., 2010, 2011; Wacker et al., 2011). The P3 and P4 are PPC sites (Amemiya et al., 2017). The PPC has also been shown to be involved in tactile motion processing (Bremmer et al., 2001; Hagen et al., 2002; Summers et al., 2009; Wacker et al., 2011; van Kemenade et al., 2014). A reference electrode was placed on the forehead. The EEG signals were amplified with a band-pass filter of 2 Hz to 2 kHz using an amplifier (Neuropack Sigma, Nihon Kohden, Tokyo, Japan). Electro-oculography (EOG) was recorded from the electrodes above and below the right eye (vertical EOG) and from each electrode lateral to each eye (horizontal EOG). A ground electrode was placed on the forehead. The EOG signals were amplified and band-pass filtered (0.08-100 Hz) using an amplifier (MEG-2100; Nihon Kohden, Tokyo, Japan). The EEG and EOG signals were digitized by A/D converters (PowerLab 800 and PowerLab 2/26, ADInstruments, Colorado, USA) with a sampling rate of 4 kHz and stored in a PC.

Procedure

Each electrical stimulus was delivered to the finger pulp through one of the four pairs of electrodes. Four stimuli were delivered, one in every 40 ms interval (Fig. 2). Thus, the time taken to complete the stimulation was 120 ms. Moving tactile stimuli were given in the P, D and R conditions (Figs. 2, 3). In the P condition, four stimuli were given in sequence from the distal to the proximal site (D1-D2-P2-P1) (Fig. 2). This stimulation pattern resulted in perception of proximally-directed movement of the tactile stimulus. In the D condition, four stimuli were delivered in sequence from the proximal to the distal site (P1-P2-D2-D1). This stimulation pattern resulted in perception of distally-directed movement of the tactile stimulus. In the R condition, four stimuli were given in the following sequence: the second proximal site (P2), the most distal site (D1), the most proximal site (P1), and the second distal site (D2) (P2-D1-P1-D2). This pattern resulted in perception of the moving tactile stimuli, but
identification of the direction of the movement was difficult. In each of the conditions (P, D and R), four sessions, each of 100 epochs, were conducted (Fig. 3). Stationary tactile stimuli were delivered in the S condition (Fig. 2). In this condition, four stimuli, one in each 40 ms interval, were delivered at one of the four sites. In the S-D1 condition, the stimuli were delivered at D1; in the S-D2 condition they were delivered at D2; in the S-P2 condition, the stimuli were delivered at P2; and in the S-P1 condition, they were delivered at P1. One hundred epochs were recorded in each condition (Fig. 3). In total, sixteen sessions were conducted in a random order. The epochs with apparent displacement of the EOG signal (i.e., displacement of the EOG signal with amplitude greater than the half of the maximum) were excluded immediately after completion of each session.

Analysis

The EEG traces between the onset of the stimuli and 300 ms after the onset of the stimuli were averaged in each stimulus condition in each electrode site in each participant (Fig. 4). The slope of the regression line for the average EEG trace in the time window of 150-200, 200-250, and 250-300 ms after the onset of the stimuli was estimated. One-way ANOVA was conducted to test the difference in the intensity at the perceptual threshold among the four stimulus sites [4 (stimulus site)]. If the ANOVA revealed a significant difference, multiple comparison (Bonferroni test) was performed. Three-way ANOVA was conducted to test the difference in the EEG slope [4 (stimulus condition) * 3 (time window) * 8 (electrode locus)]. If significant interaction among the three main effects was revealed, the test of simple interaction was conducted to test the interaction between the two main effects for each level of the other effect. If this test revealed a significant effect, the test of simple-simple main effect was conducted. If the test of simple-simple main effect revealed a significant difference, multiple comparison (Ryan’s method) was performed. The alpha level was 0.05.

Results

Perceptual threshold

Stimulus intensity at the perceptual threshold was 124 ± 11 V at the D1 electrodes, 103 ± 8 V at the D2 electrodes, 105 ± 10 V at the P2 electrodes, and 128 ± 11 V at the P1 electrodes (Fig. 5). The four pairs of electrodes were found to differ significantly in stimulus intensity at the perceptual threshold [F(3, 27) = 6.437, p = 0.002]. Multiple comparison revealed that the threshold intensity at D1 was significantly greater than that at D2, and that at P1 was significantly greater than that at P2 and D2 (p < 0.05). This finding indicates that the perceptual threshold was higher for the electrodes located at the sites peripheral to the center of the finger pulp.

Subjective perception of tactile motion

After completion of all sessions, an experimenter asked the participants about their perception of the tactile stimuli. All participants perceived the tactile stimulus motion from the distal to the proximal site of the finger pulp in the P condition, and from the proximal to the distal site of the finger pulp in the D condition.

In addition, they perceived tactile sensation moving across the stimulus sites in a random fashion in the R condition. They perceived tactile stimuli at the same site in the S condition.
As expected, no peak responses were observed in the time window between the onset and offset of the stimuli. This is likely due to the weak intensity of the stimuli. That is, a stimulus intensity around 3-4 times the perceptual threshold of the stimulus is needed to evoke SEPs (Schimsheimer et al., 1988), but the stimulus intensity in the present study was as weak as 1.1 times the perceptual threshold.

The average EEG slopes across the participants are shown in Figure 6. In the P condition, the sign of the average EEG slope was negative in the time window of 150-200 ms, positive in that of 200-250 ms, and negative in that of 250-300 ms after the onset of the stimuli at the electrodes over CP4, P4 and the right hMT+/V5. In contrast, in the D condition, the sign of the average EEG slope was positive in the time window of 150-200 ms, negative in that of 200-250 ms, and positive in that of 250-300 ms after the onset of the stimuli at the same sites.

Three-way ANOVA revealed a significant interaction between stimulus, electrode location, and time window \([F(42, 378) = 1.751, p = 0.004]\). Because of this significant interaction, the test of simple interaction was conducted to examine the interaction between the two main effects for each level of the other effect. The test of simple interaction revealed significant interactions between the effect of the stimuli and that of the time window both at P4 \([F(6, 432) = 3.358, p = 0.003]\) and at the right hMT+/V5 \([F(6, 432) = 4.853, p<0.001]\), and revealed significant interactions between the effect of stimuli and that of electrode location in the time window of 150-200 ms after the onset of the stimuli \([F(21, 567) = 2.144, p = 0.002]\) and in the time window of 200-250 ms after the onset of the stimuli \([F(21, 567) = 1.770, p = 0.019]\). Because of the significant interaction between the two main effects for the particular loci of the electrode or the particular time window, the test of simple-simple effect was conducted for each of these effects. The test of simple-simple effect revealed a significant effect of the stimuli in the time window of 150-200 ms after the onset of the stimuli at CP4 \([F(3, 648) = 3.646, p < 0.05]\). Multiple comparison revealed that the EEG slope in the D condition was significantly different from that in the P condition \([t = 3.179, p < 0.05]\) (Fig. 6). The test of simple-simple effect revealed a significant effect of the stimuli in the time window of 150-200 ms after the onset of the stimuli at P4 \([F(3, 648) = 5.650, p < 0.001]\). Multiple comparison revealed that the EEG slope in the D condition was significantly different from that in the P \([t = 4.041, p < 0.05]\), S \([t = 2.700, p < 0.05]\), and R \([t = 2.318, p < 0.05]\) conditions (Fig. 6). The test of simple-simple effect revealed a significant effect of the stimuli in the time window of 150-200 ms after the onset of the stim-

**EEG slope**

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**Figure 3 - Experimental sessions and analysis.**

**Figure 4 - An average EEG trace recorded at the site over the right hMT+/V5 in the time window of 150-300 ms after the offset of the stimuli in the D condition in one participant. The regression line is depicted in each 50 ms of the time window. The EEG slope represents the slope of this regression line. The horizontal bold lines at the bottom indicate the duration of the time window.**

**Figure 5 - Stimulus intensity at the perceptual threshold. Bars indicate means and error bars indicate standard errors of means. Asterisks indicate significant difference by multiple comparison following ANOVA \((p < 0.05)\).**

**Figure 6 - An average EEG trace recorded at the site over the right hMT+/V5 in the time window of 150-300 ms after the offset of the stimuli in the D condition in one participant. The regression line is depicted in each 50 ms of the time window. The EEG slope represents the slope of this regression line. The horizontal bold lines at the bottom indicate the duration of the time window.**
Moving tactile stimuli and cortical response

uli at the right hMT+/V5 [F (3, 648) = 6.776, p < 0.001]. Multiple comparison revealed that the EEG slope in the D condition was significantly different from that in the P [t = 4.244, p < 0.05] and S conditions [t = 2.795, p < 0.05], and the EEG slope in the R condition was significantly different from that in the P condition [t = 2.968, p < 0.05] (Fig. 6).

The test of simple-simple effect revealed a significant effect of the stimuli in the time window of 200-250 ms after the onset of the stimuli at P4 [F (3, 648) = 2.690, p < 0.05], but multiple comparison failed to reveal a significant difference between each pair of main effects. The test of simple-simple effect revealed a significant effect of the stimuli in the time window of 200-250 ms after the onset of the stimuli at the right hMT+/V5 [F (3, 648) = 4.459, p < 0.005]. Multiple comparison revealed that the EEG slope in the D condition was significantly different from that in the P [t = 2.856, p < 0.05] and S conditions [t = 2.779, p < 0.05] (Fig. 6).

The test of simple-simple effect revealed a significant effect of the stimuli in the time window of 250-300 ms after the onset of the stimuli at the right hMT+/V5 [F (3, 648) = 3.980, p < 0.01]. Multiple comparison revealed that the EEG slope in the D condition was significantly different from that in the P condition [t = 3.359, p < 0.05] (Fig. 6). Average EEG traces across the participants, especially for the D and P conditions at CP4, P4, and the right hMT+/V5, are shown in Figure 7. Some peaks were present around 200 and 220 ms after the onset of the stimuli in the P condition, and around 190 and 250 ms in the D condition for the average EEG traces across the participants. In spite of that, reproducible peaks were not found in each individual EEG trace.

Sub-condition analysis

In the S condition, the difference in the average EEG slope was tested among the S-D1, S-D2, P-D2, and P-D1 conditions (Fig. 3). The average EEG slopes across the participants are shown in Figure 8. There was a tendency for the magnitude of the EEG slope to be greatest at hMT+/V5. Nevertheless, three-way ANOVA failed to reveal significance of the main effects: stimulus [F (3, 27) = 0.486, p = 0.695], time window [F (2, 18) = 0.256, p = 0.777], and location of the electrodes [F (7, 63) = 0.904, p = 0.509]. There was no significant interaction between the main effects.

Discussion

In the present study, a tactile electrical stimulus moved across stimulus sites on the finger pulp. Given that the distribution of cutaneous receptors across the finger pulp is not uniform (Johansson and Vallbo, 1979), it may be speculated that the EEG slope is dependent on the stimulus site. The perceptual threshold differed significantly between stimulus sites in the present study; the perceptual thresholds at the distal and proximal sites were significantly higher than those at the intermediate sites. These findings seem to indicate a site dependence of tactile sensation perception across the finger pulp. On the basis of this, we performed a sub-condition analysis within the S condition to rule out the possibility that the EEG slope depends on the stimulus site. As shown in the results, there was no significant difference in the EEG slope between the four stimulus site conditions. Thus, the difference in the EEG slope between the stimulus
conditions observed in the present study is not explained by the differences in the stimulus sites. A significant difference in the EEG slope was found between the D or P condition and the S condition at the electrodes over P4 and the right hMT+/V5. This finding is consistent with a previous finding that compared the cortical activity during moving and stationary tactile stimuli (Summers et al., 2009). Nevertheless, the present and previous findings are conflicting in several respects. In previous studies, a significant difference was found in cortical activity between the moving and stationary stimuli conditions in the SI and SII contralateral to the stimulus side (Summers et al., 2009; Wacker et al., 2011), but in the present study, no significant difference in the EEG slope between the D or P condition and the S condition was found either at CP4, which is considered to be located over the SI (Ragert et al., 2011; Brodie et al., 2014), or at T3/T4, i.e., sites at which cortical responses reflect SII activity (Kany and Treede, 1997). In addition, those two previous studies found a significant difference in cortical activity between moving and stationary tactile stimuli conditions at the PPC and hMT+/V5 ipsilateral to the stimulus side (Summers et al., 2009; Wacker et al., 2011), but in the present study, no significant difference in the EEG slope between the D or P condition and the S condition was found either at P3, located over the left PPC (Amemiya et al., 2017), or at the hMT+/V5 ipsilateral to the stimulus side.

One possible explanation for the inconsistencies, between studies, with regard to the sites showing significant differences in cortical activity between the stationary and moving tactile stimulus conditions, may be due to variable intensity of the moving tactile stimulus. In the present study, the intensity of the electrical stimulus was as weak as 1.1 times the perceptual threshold, whereas a stimulus intensity around 3–4 times the perceptual threshold is needed to evoke SEPs (Schimsheimer et al., 1988). A second possible explanation is that the moving tactile stimulus is delivered bilaterally in some studies, but unilaterally in others. When the moving stimulus is delivered bilaterally, the SI, SII, PPC and hMT+/V5 are all activated (van Kemende et al., 2014). As van Kemende et al. (2014) mentioned in their study, the moving stimulus is likely enhanced when it is delivered bilaterally. Accordingly, the bilateral stimulus probably caused an even lower threshold of the cortical response, leading to activation of all sites contributing to the process of moving tactile stimulus perception. In the present study, moving tactile stimuli were delivered unilaterally. Overall, the reason for the inconsistency, across studies, in the areas activated by the moving tactile stimuli may be that some cortical areas did not reach significant levels of cortical activity when the moving stimulus was weak or unilateral.

Another possible explanation for the inconsistency is the stimulus modality. Perception of the moving tactile stimulus must be mediated by the parallel processing of two types of sensory information: spatial data, which vary with time, and direction-specific responses induced by skin stretch (Olausson et al., 1993, 2000). In previous studies investigating the cortical processing of moving tactile stimuli, mechanical stimuli, such as micro-vibration, brush stroke, air flow, or multi-pin stimulation were applied (Bremmer et al., 2001; Hagen et al., 2002; Summers et al., 2009; Wacker et al., 2011; van Kemende et al., 2014). The mechanical stimuli applied in the aforementioned studies induced perception of the moving tactile stimuli thanks not only to the spatiotemporal transition of the stimulus site but also the stretch of the cutaneous receptors. The SI, SII, bilateral anterior insula, and dorsolateral prefrontal cortex are activated during discrimination of the direction of a low friction/spatiotemporal stimulus consisting of a rolling wheel on the right thigh (Lundblad et al., 2011). On the other hand, a moving electrical stimulus on the tongue activated SII, PPC and hMT+/V5 (Matteau et al., 2010). These findings indicate that some cortical sites are commonly activated either by skin stretch or spatiotemporal transition of the stimulus site, but others are not. Thus, one possible reason why the sites activated in the present study differed from the sites activated in the other previous studies is that the present study involved only spatiotemporal transition of the stimulus site in order to induce the sensation of moving tactile stimuli. On the one hand, the difference between cortical response immediately after moving tactile stimuli and cortical response following stationary tactile stimuli reflects the cortical response both for the perception of the presence of the moving tactile stimuli and for the perception of the direction of the moving tactile stimuli. On the other hand, the difference between the cortical response after the sequentially moving tactile stimuli and that after random tactile stimuli reflects the cortical response solely to perception of the direction of the moving tactile stimuli. This is because a sensation of the direction of moving tactile stimuli is produced when the stimulus site moves in one direction throughout the stimulus period (D and P conditions), but not when the direction is changed at random within a very short period of time (each 40 ms), as in the R condition. Thus, in the present study, the significant difference in the EEG slope between the moving tactile stimuli conditions (D and P conditions) and the R condition, in which the stimulus was moved randomly, represents the perception of the direc-
Figure 8 - Average EEG slopes across participants in the sub-condition analysis of the S condition. Bars indicate means and error bars indicate standard errors of means.
tion of the moving tactile stimuli. In a previous study, a significant difference in cortical activity was found between moving tactile stimuli and random tactile stimuli at the hMT+/V5 ipsilateral to the stimulus side (Wacker et al., 2011). In the present study, the EEG slope in the D condition was significantly different from that in the R condition at P4, and that in the P condition was significantly different from that in the R condition at the electrode over the right hMT+/V5. This indicates that perception of distally-directed moving tactile stimuli is processed around the site under the electrode at the PPC contralateral to the stimulus side, but perception of the proximally-directed moving tactile stimuli is processed around the site under the electrode at the hMT+/V5 contralateral to the stimulus side.

The main finding of the present study was the presence of a direction-specific cortical response immediately after moving tactile stimuli. As shown in the EEG traces, the plus/minus sign of the EEG slope was inverse between the D and P conditions in each time window. In the time window of 150-200 ms after the onset of the stimuli, the average EEG slope in the D condition was significantly different from that in the P condition at the electrodes over the CP, P4 and right hMT+/V5. Direction-specific activity of moving tactile stimuli has been observed in the SI and SII (Wacker et al., 2011). The hMT+/V5 has been shown to contribute to discrimination of the direction of a moving tactile stimulus (Amemiya et al., 2017). In spite of those previous findings, the present study is the first to show that moving tactile stimuli cause a direction-specific cortical response recorded at the electrodes over the PPC and hMT+/V5 contralateral to the stimulus side.

These findings indicate that the cortical response immediately after distally-directed moving tactile stimuli is different from the cortical response after proximally-directed moving tactile stimuli at those sites. At the electrode over the right hMT+/V5, the EEG slope was significantly different between the D and P conditions across all time windows, and the magnitude of the EEG slope at the electrode over the right hMT+/V5 was the largest among the electrode sites. These findings indicate that the cortical region where direction-specific cortical responses are generated immediately after moving tactile stimuli is located near the hMT+/V5 contralateral to the stimulus side. The activity of some populations of SI neurons depends on the direction of the moving tactile stimulus in monkeys (Ruiz et al., 1995). In humans, direction-dependent cortical activity is present at the SI and SII during moving tactile stimulus (van Kemenade et al., 2014). However, such direction-dependent cortical activity was not revealed in the hMT+/V5 (van Kemenade et al., 2014). TMS over both the SI and hMT+/V5, but not the PPC, significantly reduced tactile discrimination (Amemiya et al., 2017). However, these findings do not constitute a demonstration of direction-specific cortical activity in response to moving tactile stimuli; rather, they indicate the site of cognitive processing for discriminating the direction of these stimuli. Accordingly, the present finding is first evidence of a direction-specific cortical response occurring immediately after moving tactile stimuli recorded at the electrode over the hMT+/V5 contralateral to the stimulus side. Motion processing occurs at hMT+/V5 (Sack et al., 2006; Matteau et al., 2010). Accordingly, the present finding that the greatest direction-specific response immediately after the moving tactile stimuli is observed at the electrode over the hMT+/V5 may reflect motion processing.

In previous studies, significant cortical activity during moving tactile stimuli or during discrimination of the direction of moving tactile stimuli was present not only in the hemisphere contralateral to the stimulus side, but also in the hemisphere ipsilateral to the stimulus side (Bodegård et al., 2000; Hagen et al., 2002; Summers et al., 2009; Wacker et al., 2011; van Kemenade et al., 2014). By contrast, in the present study, the significant difference in the EEG slope after the offset of the stimuli between the stimulus conditions was revealed particularly at the electrode sites contralateral to the stimulus side. This finding indicates that moving tactile stimuli cause the cortical response, particularly in the hemisphere contralateral to the stimulus side.

In conclusion, a direction-specific EEG response immediately after the onset of moving tactile stimuli arises at the electrode sites over the SI, PPC, and hMT+/V5 contralateral to the stimulus side in healthy female humans. The direction-specific EEG response immediately after the offset of the moving tactile stimuli is generated from the cortical region around the hMT+/V5 contralateral to the stimulus side. The direction-specific EEG response immediately after perception of tactile motion, found in the present study, may be useful for evaluation of the somatosensory function in patients with tactile sensory disturbances. Moreover, the EEG slope immediately after the moving tactile stimuli could be used in biofeedback training to promote recovery of tactile motion sensation in patients with tactile sensory disturbances.

References


Moving tactile stimuli and cortical response