

EEG correlates of haptic feedback in a visuomotor tracking task

Chun-Ling Lin^{a,b,d}, Fu-Zen Shaw^c, Kuu-Young Young^b, Chin-Teng Lin^{a,b,d,e,*}, Tzzy-Ping Jung^{a,d,e,**}

^a Brain Research Center, University System of Taiwan, Hsinchu, Taiwan

^b Department of Electrical and Control Engineering, National Chiao-Tung University, Hsinchu, Taiwan

^c Department of Psychology, National Cheng Kung University, Tainan, Taiwan

^d Institute for Neural Computation, University of California, San Diego, CA, USA

^e Institute of Engineering in Medicine, University of California, San Diego, CA, USA

ARTICLE INFO

Article history:

Received 29 September 2011

Revised 22 December 2011

Accepted 4 February 2012

Available online 13 February 2012

Keywords:

Visuomotor tracking task

Electroencephalogram (EEG)

Haptic feedback

Independent component analysis (ICA)

Time–frequency analysis

Event-related coherence (ERCOH)

ABSTRACT

This study investigates the temporal brain dynamics associated with haptic feedback in a visuomotor tracking task. Haptic feedback with deviation-related forces was used throughout tracking experiments in which subjects' behavioral responses and electroencephalogram (EEG) data were simultaneously measured. Independent component analysis was employed to decompose the acquired EEG signals into temporally independent time courses arising from distinct brain sources. Clustering analysis was used to extract independent components that were comparable across participants. The resultant independent brain processes were further analyzed via time–frequency analysis (event-related spectral perturbation) and event-related coherence (ERCOH) to contrast brain activity during tracking experiments with or without haptic feedback. Across subjects, in epochs with haptic feedback, components with equivalent dipoles in or near the right motor region exhibited greater alpha band power suppression. Components with equivalent dipoles in or near the left frontal, central, left motor, right motor, and parietal regions exhibited greater beta-band power suppression, while components with equivalent dipoles in or near the left frontal, left motor, and right motor regions showed greater gamma-band power suppression relative to non-haptic conditions. In contrast, the right occipital component cluster exhibited less beta-band power suppression in epochs with haptic feedback compared to non-haptic conditions. The results of ERCOH analysis of the six component clusters showed that there were significant increases in coherence between different brain networks in response to haptic feedback relative to the coherence observed when haptic feedback was not present. The results of this study provide novel insight into the effects of haptic feedback on the brain and may aid the development of new tools to facilitate the learning of motor skills.

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Introduction

Learning a new movement or motor skill utilized in our daily lives is often guided by external stimuli and feedback (Blum et al., 2007; Grindlay, 2007). Previous studies have shown that the association of external stimuli with motor commands is useful for motor learning; thus, systematic practice can improve an individual's performance (Maxwell et al., 2001; Schmidt and Wulf, 1997). An external stimulus usually originates from an outside source. The external stimulus is an alternative to an intrinsic stimulus related to an individual's sensory-perceptual information (Wolpert et al., 2001; Yamagishi et al., 2001). Intrinsic stimuli often involve three primary communication

channels: visual, auditory, and tactile (Hawk and Shah, 2007; Williams, 1983). In contrast, external stimuli can assume many forms in motor learning applications, including verbal communication and visual, auditory, tactile, and haptic signals (Deutsch et al., 2004; Lee et al., 1990; Lieberman and Breazeal, 2007; Merians et al., 2002; 2006; Millar and Al-Attar, 2004). In addition, Brosvic et al. (2010) suggested that novices could rapidly improve their performance when provided with immediate feedback and more specific information regarding error correction.

In recent years, electroencephalograms (EEGs) have increasingly been utilized as a means to study the neuronal mechanisms underlying behavioral changes associated with the acquisition of motor skills (Hatfield et al., 2004; Hillman et al., 2000). EEG frequencies of interest vary in relation to the actual physiological and psychological brain state (Jancke, 2005). Pre-stimulus theta (4–8 Hz) and alpha (8–12 Hz) activities reflect pre-stimulus top-down preparation for the performance of subsequent tasks (Min and Park, 2010). Recent studies have revealed that movement, speed and direction could be decoded by low-frequency modulation (in the range of delta and low theta bands; <7 Hz) during the execution of movement

* Correspondence to: C.-T. Lin, Brain Research Center, National Chiao-Tung University (NCTU), 1001 Ta-Hsueh Road, Hsinchu 300, Taiwan. Fax: +886 3 572 6272.

** Correspondence to: T.-P. Jung, Swartz Center for Computational Neuroscience, Institute for Neural Computation, University of California, San Diego, 9500 Gilman Dr. #5059, La Jolla, CA 92093-0559, USA. Fax: +1 858 822 7556.

E-mail addresses: ctlin@mail.nctu.edu.tw (C.-T. Lin), jung@sccn.ucsd.edu (T.-P. Jung).

(Acharya et al., 2010; Waldert et al., 2008). Perfetti et al. (2011a) also found that initial visuomotor learning was associated with the enhancement of gamma (> 30 Hz) power during movement execution as well as gamma/theta phase coherence during movement planning. Late-stage learning was accompanied by an increase of theta power during movement planning, which was correlated with the degree of learning and retention. Furthermore, Perfetti et al. (2011a) suggested that delta, alpha and gamma phase coherences were related to motor and sensory demand during motor learning. Smith et al. (1999) reported a task-specific enhancement of alpha activity over somatomotor areas when preceded by several days of practice with a visuomotor tracking task; however, the augmented alpha activity was diminished after the subjects mastered the task. These investigators concluded that regional alpha-power changes might reflect the development of task-specific neurocognitive strategies. Other studies found that there were movement-related power and coherence changes in the beta (13–30 Hz) band during the initial learning of a motor task (Mima et al., 2000; Serrien and Brown, 2002; 2003). Furthermore, some studies have suggested that the cortical beta amplitude co-varies with motor performance (Boonstra et al., 2007; Toma et al., 2002). Boonstra et al. (2007) reported an enhancement of event-related alpha desynchronization during implicit motor skill learning, increased cortico-spinal beta synchronization following visuomotor skill learning and increased inter-hemispheric synchronization during early stages of bilateral learning. Other studies suggested that visuomotor skill learning is related to long-range oscillatory neuronal synchronization in the beta and gamma frequency ranges (13–80 Hz) (Babiloni et al., 2006; Huo et al., 2011; Lee, 2003). Ng et al. (2011) further extended the connection between beta- and gamma-band rhythms and motor behaviors. Task-dependent gamma activity is related to various types of cognitive processes, including attention, motor planning, visual processing, working memory (WM) and long-term memory (LTM) (Meeuwissen et al., 2011). However, most prior studies have employed visual and/or auditory feedback to provide continuous guidance for motor commands (Blum, 2008; Blum et al., 2007, 2008). Haptic feedback is now receiving increasing attention related to motor-skill learning due to its novelty and potential for real-world applications (Perrin et al., 2008). Importantly, no EEG study reported to date has explored the temporal brain dynamics and interactions between different brain regions during motor skill learning in conjunction with haptic feedback.

To coordinate an individual's sensory perception with imminent external stimuli, extensive transformation and integration processes are required. In this regard, different brain regions are assumed to constitute a cooperative network that facilitates the synchronization of task-specific brain activities (Blum, 2008; Blum et al., 2008). Such cooperation between brain regions has been studied using coherence and phase-locking analysis of EEG signals (Blum, 2008; Blum et al., 2007, 2008; Classen et al., 1998; Lehmann et al., 2006). However, previous studies have analyzed coherence and phase-locking measures on the basis of confounded mixed EEG signals recorded from the scalp. Such measurements could not specifically represent the relationship between different brain areas because the recording from each electrode incorporated contributions from several brain sources. Zervakis et al. (2011) also suggested that the separation, identification and analysis of independent activities of different brain regions are critical for characterization of the neurophysiological origins of the brain processes in question. Therefore, separating the recorded signals into independent brain source activities is an important first step toward relating a specific task (sensory, motor or cognitive) with the topography and/or time–frequency content of the brain sources (Gwin et al., 2010; Jung et al., 2001; Lee et al., 2003; Zervakis et al., 2011). In these studies, independent component analysis (ICA) (Bell and Sejnowski, 1995; Makeig et al., 1997) was utilized to decompose recorded EEG signals into temporally independent

components. Time–frequency analysis and the topographic origins of components were then used to characterize event-related brain dynamics.

The present study is also focused on event-related changes in the coupling of field activity in different regions of the cortex (Sarnthein et al., 1998). Recent results from several datasets have indicated that maximally independent EEG signals can be rapidly synchronized and desynchronized following significant task events (Delorme and Makeig, 2004; Makeig et al., 2002). The structure of EEG synchronization events, as revealed by ICA, is largely or wholly invisible to analyses based on average measures of evoked responses or scalp channel coherences. In the present study, the independent brain sources separated by ICA were then analyzed by time–frequency analysis and event-related coherence (ERCOH) to observe brain activities during tracking tasks in the presence and absence of haptic feedback.

Previous studies have suggested that practice and learning would increase coherence between the participating brain regions (Andres et al., 1999; Serrien and Brown, 2003; Singer, 1993; Singer and Gray, 1995). Because non-haptic feedback trials rely solely on internal movement representation, this study addresses the hypothesis that the ERCOH of these trials would be smaller than those of haptic trials.

Methods and materials

Subjects

A total of 19 right-handed volunteers (9 females and 10 males; mean age 23 ± 4 years) with normal or corrected-to-normal vision participated in the experiment. In the experiment, the subjects used their dominant (right) hands to control a joystick. All subjects were healthy and had no history of neurological disease. To obtain an accurate evaluation of their performance, the subjects were required not to have imbibed alcoholic or caffeinated drinks or to have participated in strenuous exercise 1 day prior to the experiments. The Institutional Review Board of Taipei Veterans General Hospital approved the experimental protocol used in this study. The participants were subjected to the experiments either in the morning (9–12 AM) or afternoon (2–5 PM). Each subject was well instructed regarding the experimental procedures, and none of the participants were aware of the hypotheses being tested. All subjects delivered their informed consent prior to any experimentation.

Experimental equipment

The basic principle of the tracking task used in this study was aimed at increasing the subjects' tracking precision. In the tracking paradigm, all subjects sat in front of a 19" monitor (resolution of 1024×768 pixels) and learned to control a joystick (Immersion Impulse Stick, USA, Fig. 1C) to minimize the deviation between a green cross and a moving target stimulus (a purple trajectory), as shown in Fig. 1A). The purple trajectory was a straight line (6×35 pixels) and appeared when the task started, first at the upper-right corner of the box frame. To control the speed of the subject's movement, the purple trajectory moved at a constant velocity. The subjects maneuvered a green cross to closely follow the purple trajectory in an 80-pixel-thick black frame in the shape of a large box frame (660×660 pixels, Fig. 1B). The movement that took place in this experiment was therefore simple and one-dimensional. A shelter was used to prevent subjects from watching their hands and avoiding the screen as they controlled the joystick (Fig. 1B). Furthermore, an armrest was designed to make the subjects comfortable with control of the joystick (Fig. 1C).

The joystick employed in the experiments provided two force feedback axes and movement of up to three degrees of freedom. The joystick used electric motors that could be programmed to

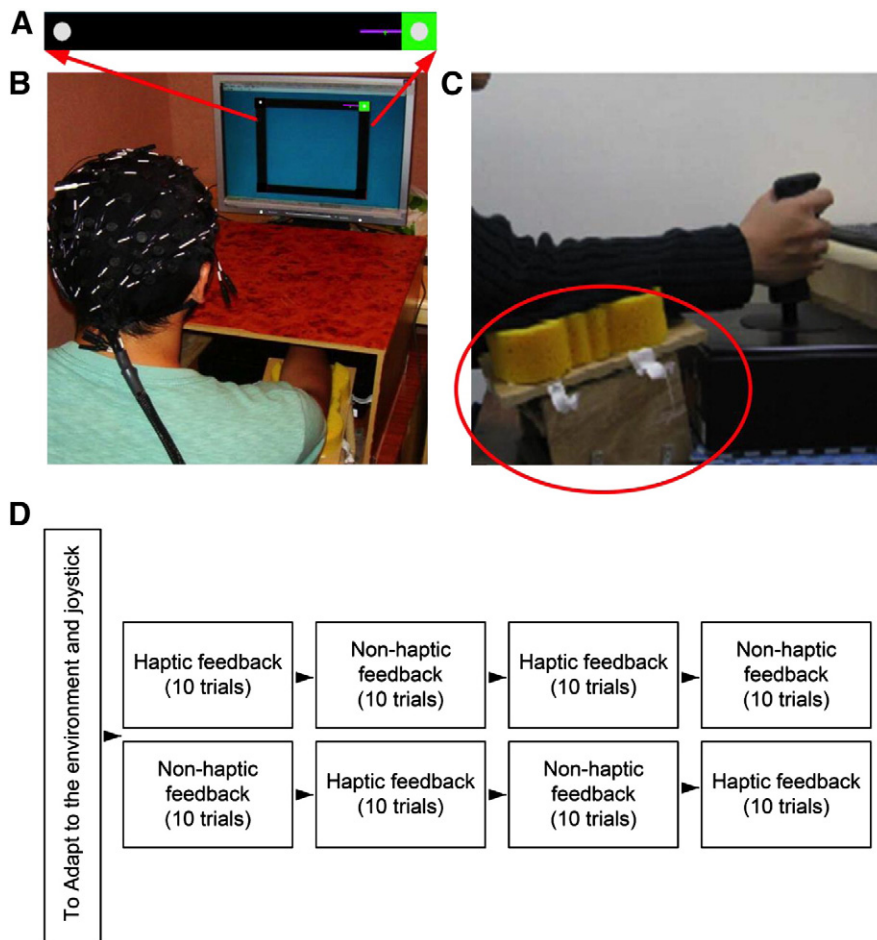


Fig. 1. The experimental environment and a schematic diagram of the experimental paradigm. (A) In the tracking task, all subjects learned to control the joystick to minimize positional deviation between a green cross and a constantly moving stimulus (the purple trajectory). (B) The backdrop of each experiment consisted of a square frame (660×660 pixels) with a black border (80 pixels) that was presented at the center of a computer screen. A shelter was used to deter subjects from watching their hands instead of the screen when controlling the joystick. (C) An armrest was used to minimize hand fatigue among subjects. (D) The experiment was comprised of four blocks of 10 trials, and each block involved only one condition (either with or without haptic feedback). Each subject was randomly assigned to one of the experimental conditions (I or II).

produce forces as large as 14.5 N (3.5 lbf) and could move to a desired position with a resolution of 0.01° . It was a robust joystick that was designed for rugged applications, including entertainment and industrial control. The device had an on-board microprocessor to load and play haptic effects as frequently as 100 times per second. Joystick control was established using Windows DirectX (Windows) and Immersion I-Force 2.0 Compatible (Immersion) in combination with Microsoft Foundation Class (MFC) and Open Graphics Library (OpenGL). The joystick employed a universal serial bus (USB) interface. The Software Development Kit (Windows) can be used as a tool for real-time graphical development and testing of this device.

In this study, this force-feedback joystick was used to apply forces that assisted the subjects in following the purple target trajectory. Because the width of the purple trajectory was 6 pixels, absolute deviations between the green cross and the desired trajectory of less than 3 pixels were disregarded as non-tracking errors. In contrast, the force feedback mechanism was activated when the absolute deviation between the green cross and the desired trajectory was greater than 3 pixels, and the amount of force applied was linearly proportional to the deviation. We described the relationship between the magnitude of the deviation in tracking and the magnitude of the feedback force provided by the joystick via the following equation:

$$F = (D-3), \text{ when } D > 3,$$

where D is the magnitude of the deviation in tracking, and F is the magnitude of the feedback force provided by the joystick.

Experimental paradigm

Each trail had four initial starting points, which were located at the four corners of the box frame. The upper-right corner of the box frame was the first starting point, after which the sequence of the starting points proceeded in a counter-clockwise direction. At the beginning of each starting point, the color of the square turned black for 3.2 s, and the subjects were instructed to keep the green cross inside a white circle (a baseline period). Subsequently, the color of the square turned yellow for 0.8 s, signaling the initiation of the tracking task (a cue period). Once the color of the square turned green (task onset), the subjects began adjusting the joystick to maneuver the green cross along the purple trajectory, which moved at a constant speed along the frame for approximately 6.2 s. The purple trajectory disappeared once the green cross reached the white circle of the next starting point (task offset). Each experiment consisted of 45 tracking trials.

For each subject, the first five tracking trials were used as training sessions. The subsequent 40 trials were divided equally into four blocks. To understand the effects of haptic feedback on motor learning, in half of the trials ($n=20$), the subjects received haptic

feedback. The sequences of the haptic and non-haptic feedback trials were counter-balanced across subjects (Fig. 1D, I or II).

The subjects were given 2–6 min short breaks between two blocks according to the level of fatigue they experienced. The entire experiment took approximately 1 h/participant.

Data acquisition

EEG measurements provide a non-invasive method for recording the voltage differences of scalp potentials (Thompson et al., 2008) and can be used to examine brain dynamics during cognitive experiments. The experimental environment was surrounded by a Faraday cage to protect the EEG equipment from electromagnetic noise. In this study, sixty-four channel EEG data were amplified (NuAmps, Compumedics Ltd., VIC, Australia), sampled at 1 kHz, digitized using a 32-bit quantization level, and notch filtered at 60 Hz. The contact impedance between the scalp and the electrode was calibrated to be less than 10 k Ω using conductive gel. At the beginning of the experiment, the locations of each electrode were digitized using a 3D digitizer (POLHEMUS 3 space Fastrak).

During the experiments, the position of the green cross was continuously recorded while the joystick was in use, which was in turn synchronized to the EEG signals. The green cross position data were sampled and digitized at 64 Hz with a 0.01-degree position resolution. The digitized positions of the green cross (recorded in pixels) were transferred via a USB interface to a personal computer (PC) for storage.

Analysis of behavioral data

This study defined two indices to evaluate the tracking performance of participants: tracking errors and the number of adjustments. The tracking error statistic measured absolute deviations between the target purple trajectory and the actual location of the green cross at any given time. In this study, the subject was instructed to control the joystick to track the target purple trajectory as closely as possible. Each adjustment of the joystick was counted. Within a single trial, four averaged tracking errors and numbers of adjustments corresponding to the 4 segments along the box frame were extracted for statistical testing between haptic and non-haptic conditions.

EEG data analysis

EEG signals were analyzed using MATLAB (The Mathworks, Inc.) and the open source toolbox EEGLAB (Swartz Center for Computational Neuroscience, La Jolla, CA; <http://www.sccn.ucsd.edu/eeGLAB>). Raw EEG data were filtered with a 50 Hz low-pass filter and a 2 Hz high-pass filter to remove line noise (60 Hz and its harmonic) and DC drifts. Subsequently, the EEG data were down-sampled to 250 Hz for data compression. For each single trial, four epochs corresponding to the 4 segments of the box frame were extracted from continuous EEG signals. Each epoch contained a 10.5-s EEG segment (epoch; from 1.5 s before to 9 s after the cue onsets) and three events (cue, task onset and task offset). The aim of the present study was to investigate the differences in brain activities between epochs with and without haptic feedback. Epochs in which the subjects did not make tracking errors above the established threshold (3 pixels) were excluded from further analysis, as the feedback would not have been administered to the subjects. For all subjects tested, the average proportion of epochs with no tracking errors was 55%. Although the EEG assay was designed to record cerebral activity, it also recorded electrical activities arising from sites other than the brain. The recorded activity that was not of cerebral origin was designated as an artifact of the recording process. The amplitude of artifacts could be quite large relative to the amplitudes of the cortical signals of interest and could be divided into biological and environmental

artifacts (Mantini et al., 2008). Some of the most common biological artifacts included eye-induced, ECG, EMG and Glossokinetic artifacts. Environmental artifacts often originated from outside the body (e.g., due to movement by the subject or spikes originating from a momentary change in the impedance of a given electrode). Therefore, epochs containing the aforementioned artifacts were also rejected by visual inspection using the EEGLAB visualization tool, which was used to enhance SNR prior to further analysis.

Independent component analysis

This study applied independent component analysis to decompose the recorded EEG signals into temporally independent time courses presumably arising from distinct brain sources (Bell and Sejnowski, 1995; Makeig et al., 1997) using EEGLAB (Delorme and Makeig, 2004). The use of ICA to decompose EEG data is based on two premises: (1) EEG data recorded at multiple scalp electrodes are linear sums of temporally independent sources arising from spatially fixed brain or extra-brain networks; and (2) the spatial spread of the electric current from sources via volume conduction does not involve significant time delays (Jung et al., 2001). The ICA algorithm can separate N source components (independent components) from N channels of EEG signals. The obtained multi-channel EEG recordings are considered to be mixtures of underlying brain sources and artifactual signals. The source signals contribute to the scalp EEG signals through a linear mixing filter. The mixing process can be reverted via an unmixing matrix, \mathbf{W} , in $\mathbf{u} = \mathbf{W}\mathbf{x}$, where \mathbf{u} is the source matrix, and \mathbf{x} is the scalp-recorded EEG. The mixing filter can be plotted as the scalp topography of the independent component. Independent components (IC) accounting for blinks, eye moments, and muscle activity were visually identified and then removed from subsequent analyses.

The scalp topography of each independent component of ICA can be further analyzed using DIPFIT2 routines (Oostenveld and Oostendorp, 2002), which are an EEGLAB plug-in, to find the 3D location(s) of an equivalent dipole(s) based on the locations of the electrodes, which were digitized by the 3D digitizer. The components across 19 subjects with similar scalp topographies, dipole locations and event-related spectral perturbations (ERSPs) were further grouped into a component cluster using a *study* function found as an EEGLAB plug-in (Delorme and Makeig, 2004; Gramann et al., 2010; Makeig et al., 2002). In this study, the parameters in the *study* function were determined based on empirical evaluations and suggestions from the original development team as well as those of advanced users and EEGLAB instructors (via personal communication; Chiu et al., 2011; Delorme and Makeig, 2004; Gramann et al., 2010; Onton et al., 2005). First, we compressed and combined each IC measure into a 10-dimensional measure (except for dipole locations with three dimensions: x , y , z) by principal component analysis (PCA), resulting in a 23-dimensional combined measure. Subsequently, the three-dimensional feature of the dipole locations was multiplicatively weighted by a factor of 10. Principal components of ERSPs assigned a weight of 3, and those of scalp topographies were given a weight of 5. Finally, ICs were clustered by applying the K-means algorithm to the 23-dimensional measure to obtain clusters with the greatest possible distinction by minimizing the variability within and the maximizing variability between clusters. ICs with a distance larger than three standard deviations from the mean of any cluster centroid were removed and not analyzed.

Time–frequency analysis and event-related spectral perturbations (ERSPs)

Time–frequency analysis was employed to test the dynamics of the component power spectra. Time–frequency analysis was performed for all of the components by convolving single-epoch data with Hanning-window sinusoidal wavelets (Delorme and Makeig, 2004). For each selected epoch for which the tracking error was greater than 3 pixels regardless of feedback delivery, the mean

baseline log power spectrum was subtracted from the spectral estimate to produce a baseline-normalized time–frequency representation. The duration of the baseline period ranged from -1.5 to 0 s with respect to the cue onsets. Although a purple trajectory with a constant speed was used to control the speed of movement among subjects, the task offset of the epochs varied among the participants. Thus, the time–frequency estimates were processed using a time-warped procedure to obtain consistent temporal lengths for the time–frequency estimates ($n = 200$ pts). The time-warped procedure was performed in EEGLAB and was used to linearly transform the time–frequency estimates to normalize the time length difference between each epoch (Chiu et al., 2011). The time–frequency estimates of all epochs were linearly stretched or compressed to align the events (cue, task onset and task offset) and to split the component activities into three disjointed phases: (1) the baseline period, in which the 0 to 50th data points corresponded to the baseline period of the original epoch; (2) the cue period, in which the 51st to 80th data points represented the period ranging from the cue onset to the task onset; and (3) the task period, in which the 80th to 195th data points accounted for the period ranging from the task onset to the task offset. The time-warped procedure enabled direct comparison of all epochs regardless of the differences in event latencies and durations. Event-related spectral perturbation (Makeig, 1993) images were then constructed to assess the statistical significance of the changes (in dB) from the mean baseline in spectral power across a broad frequency range (2–50 Hz). The ERSP images for trials with and without haptic feedback were calculated and plotted separately and are shown in Figs. 4–9.

Event-related coherence (ERCOH)

This study also addresses event-related changes in the coupling of field activity in different regions of the cortex (Sarnthein et al., 1998). Several datasets have revealed that maximally independent EEG signals may be rapidly synchronized and desynchronized following significant task events (Delorme and Makeig, 2004; Makeig et al., 2002). This study computes ERCOH between two component activities in a

set of similar event-related epochs to determine the degree of synchronization of the two component processes at each frequency and latency. The magnitudes of ERCOH vary between 0 and 1, where 0 indicates a complete absence of synchronization, and 1 indicates perfect synchronization.

Statistical analyses

Statistical analyses were performed using MATLAB. We employed a non-parametric bootstrap statistical method for determining the significance between differences in components' ERSPs ($\alpha < 0.05$). Specifically, we first divided the component time/frequency features of all epochs into 2 conditions (in this case, haptic vs. non-haptic). For each condition, these features were randomly and repetitively shuffled and then partitioned into two series of the same size as the original series. Applying the original operation to these shuffled series (i.e., for time–frequency decomposition and the simple mean of the time–frequency decomposition of a single epoch) produced a probability distribution of the obtained values. If measurements of non-shuffled data fell within this distribution, the series were not considered to be significantly different. For each subject, we averaged the tracking errors and number of adjustments in response to both haptic and non-haptic feedback conditions separately. Subsequently, a paired-sample *t* test was performed to identify significant differences in the tracking errors and numbers of adjustments between the two conditions. A paired-sample Wilcoxon signed-rank test was applied to the EEG measures to assess the statistical significance of the differences between haptic and non-haptic feedback. The level of significance was set at $p < 0.05$.

Results

Comparison of behavioral performance between epochs with and without haptic feedback

Fig. 2 shows the mean and standard deviation (SD) of the tracking errors and numbers of adjustments made by subjects during tracking

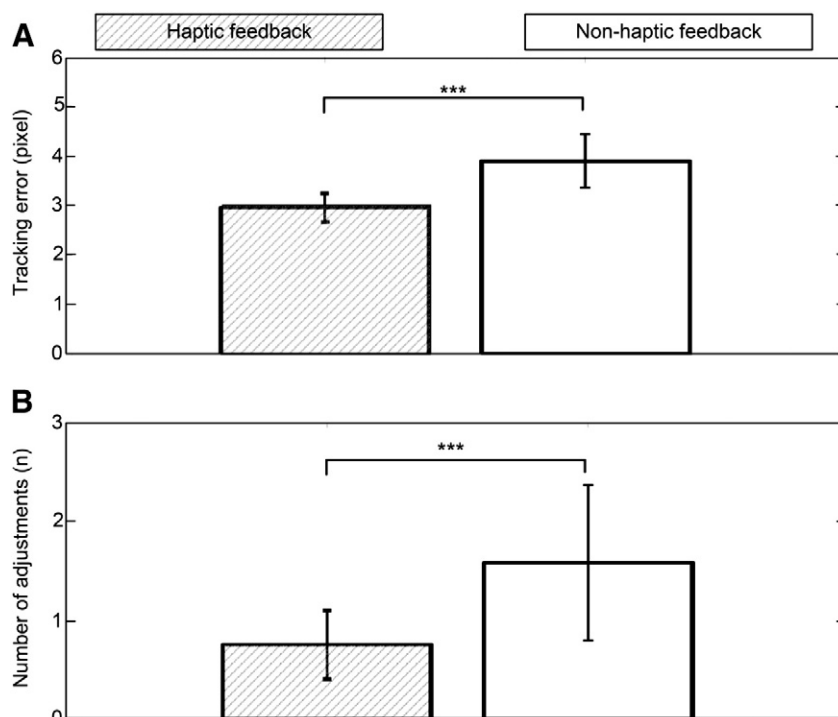


Fig. 2. Mean and standard deviation of tracking error and the number of adjustments across subjects. Oblique line blocks represent epochs with haptic feedback, and blank space blocks represent epochs without feedback. Statistical test results are noted as * $p < 0.05$; ** $p < 0.01$; and *** $p < 0.001$.

experiments with and without haptic feedback. A paired-sample *t* test revealed that the differences in tracking errors between haptic and non-haptic conditions were statistically significant (3.05 ± 0.31 vs. 3.90 ± 0.54 ; $P < 0.001$; Fig. 2A). The differences in the numbers of adjustments between epochs with and without haptic feedback were also statistically significant (0.76 ± 0.34 vs. 1.58 ± 0.78 , $P < 0.001$; Fig. 2B). In summary, the behavioral results demonstrated that the tracking errors and number of adjustments in epochs with haptic feedback were significantly smaller than in those without feedback.

EEG dynamics correlated with haptic feedback

After removing bad channels and sections of data with uncharacteristic artifacts, ICA was used to decompose the remaining EEG data (>95%) into spatially fixed and temporally independent components. DIPFIT2 routines from EEGLAB were then used to fit one, or occasionally two, nearly bilaterally symmetric dipole models to the scalp topography of components using the locations of the digitized electrodes. The ICs for all subjects were then clustered according to the correlations among their scalp topographies, dipole locations and time–frequency characteristics. Fig. 3 shows the mean scalp maps of eight component clusters from 19 subjects and their equivalent dipole sources located in or near the medial frontal ($n = 16$), left frontal ($n = 11$), central ($n = 22$), left motor ($n = 21$), right motor ($n = 11$), parietal ($n = 27$), left occipital ($n = 7$) and right occipital ($n = 9$) regions.

Spectral changes under different conditions

To quantitatively assess the differences between the EEG activities associated with epochs with and without haptic feedback, ERSPs were plotted (see the **Methods and materials** section) under different conditions. Among eight IC clusters, six (i.e., the left frontal, central, left motor, right motor, parietal and right occipital component clusters) showed statistically significant differences in spectral power between epochs with and without haptic feedback during the task period; in contrast, the remaining two component clusters (i.e., medial frontal and left occipital) did not. Fig. 4 shows the mean scalp map and activity patterns of a cluster of 11 components (from 19 subjects) that projected most strongly to the left frontal scalp sites. The mean ERSPs of the left frontal component cluster for epochs with and without haptic feedback (Fig. 4B) revealed a theta power increase that was time locked to cue onsets and a decrease in both alpha power and beta power during the task period. Fig. 4C shows the average power spectrum density (PSD) of epochs with and without haptic feedback during the task period.

Similarly, Figs. 5–9 show the mean scalp maps and activity patterns of the central, left motor, right motor, parietal and right occipital component clusters. Relative to the baseline power, the ERSPs of these component clusters also exhibited a theta power increase that was time locked to the cue onsets and decreases in delta power, alpha power, beta power, and gamma power during the task period. The ERSPs of the left motor, right motor, parietal and right occipital component clusters exhibited an alpha-power decrease after the aforementioned theta power increase.

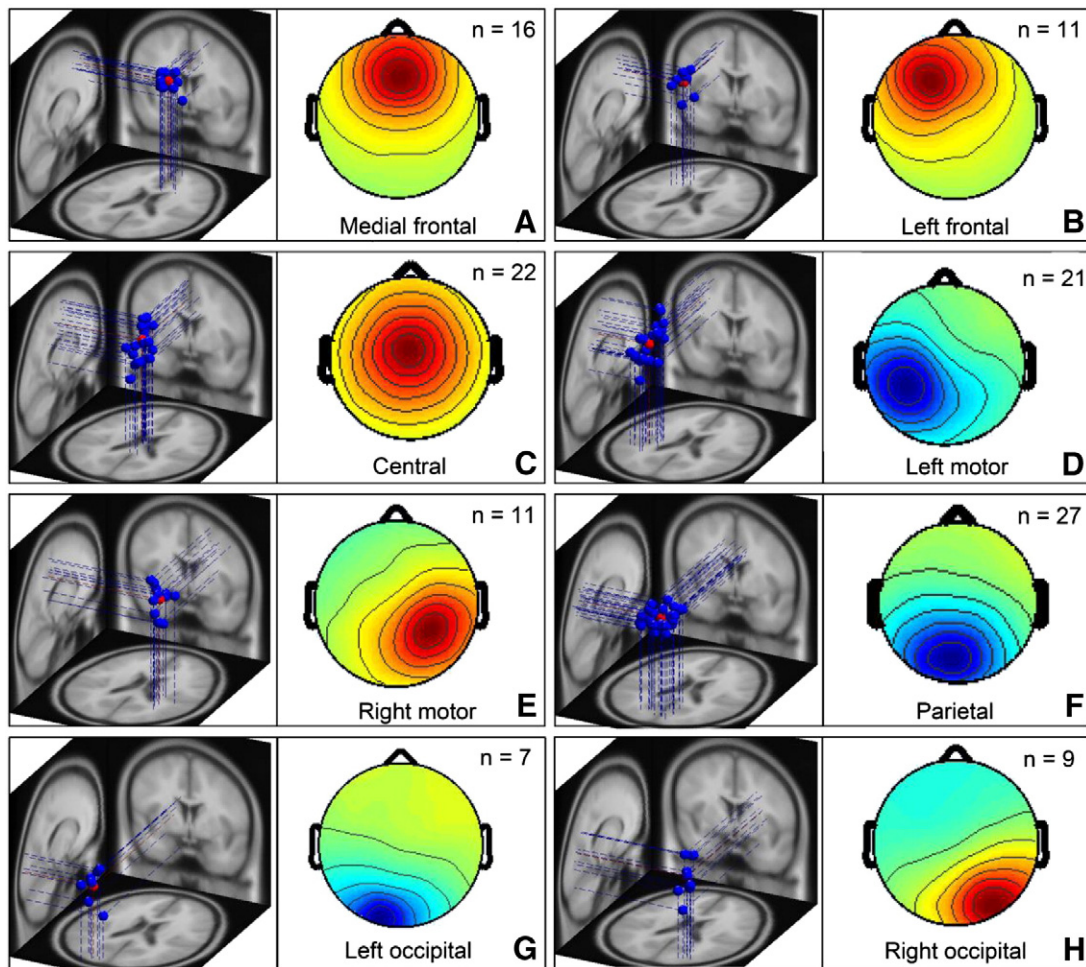


Fig. 3. Equivalent dipole source locations and mean scalp maps for eight component clusters from 19 subjects. The 3D dipole source locations and their projections onto average brain images are given in the left panels of each cluster. The averaged scalp maps are shown in the right panels of each cluster. (A) Medial frontal ($n = 16$), (B) left frontal ($n = 11$), (C) central ($n = 22$), (D) left motor ($n = 21$), (E) right motor ($n = 11$), (F) parietal ($n = 27$), (G) left occipital ($n = 7$) and (H) right occipital ($n = 9$) component clusters.

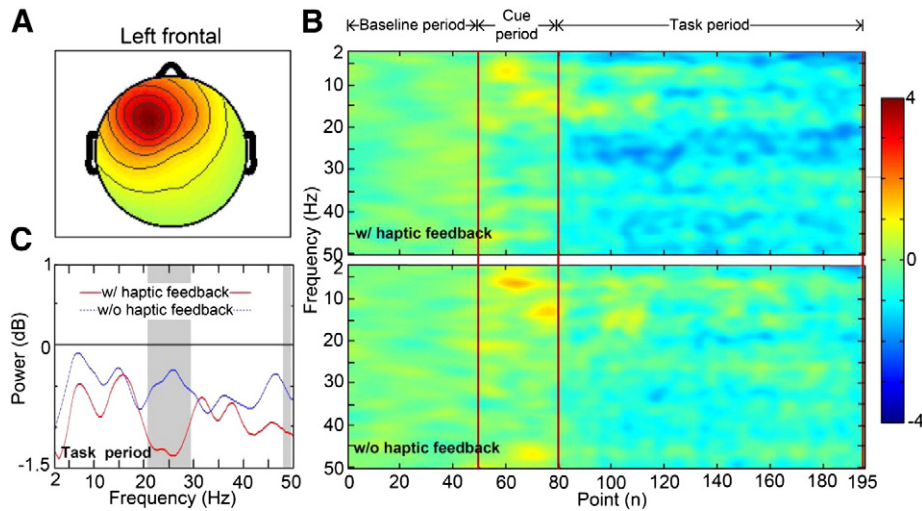


Fig. 4. The mean scalp maps, averaged group time–frequency responses and spectral changes of a left frontal component cluster during a visuomotor tracking task.

The gray bars in Figs. 4–9C indicate the frequency bins in which the PSD of the components differed significantly between haptic and non-haptic feedback during the task period ($p < 0.05$, as determined by a paired-sample Wilcoxon signed-rank test). For all subjects, components with equivalent dipoles in or near the right motor areas exhibited greater alpha band power suppression, while components with equivalent dipoles in or near left frontal, central, left motor right motor and parietal regions exhibited greater beta-band power suppression. Additionally, components with equivalent dipoles in or near the left frontal, left motor and right motor regions showed greater gamma-band power suppression when subjects received haptic feedback, compared to the non-haptic condition. In contrast, the right occipital component cluster exhibited less beta-band power suppression in epochs with haptic feedback relative to the non-haptic condition.

Event-related coherence (ERCOH) between different component activities

To examine event-related changes in the coupling of EEG activity between different brain regions, we analyzed ERCOH between the activities of different component clusters. Fig. 10A–F compares ERCOH between different clusters for epochs with (solid red line) and without (dashed blue line) haptic feedback during the task

period. The gray bars in Fig. 10A–F denote the frequency bins in which ERCOH values differed significantly between the two conditions ($p < 0.05$, as determined by the paired-sample Wilcoxon signed-rank test). In all of these frequency bins, epochs with haptic feedback presented higher ERCOH values between component clusters compared to those without haptic feedback. In particular, the coherence between the parietal and right motor component clusters was significantly higher in the delta, theta, beta and gamma frequency bins in epochs with haptic feedback. At the same time, ERCOH between the central region and two other ICs (the parietal and right motor regions) showed a significant increase in the theta band. ERCOH between the central region and three other ICs (the left frontal, parietal and right motor regions) exhibited significant increases in the beta band, while ERCOH between the left motor region and two other ICs (the right motor and right occipital regions) exhibited significant increases in the beta bands. ERCOH between the left motor region and two other ICs (the right motor and parietal regions) presented a significant increase in the alpha band. Finally, ERCOH between the central region and two other ICs (the left frontal and right motor regions) and ERCOH between the parietal and right occipital regions showed a significant increase in the gamma band. Fig. 10G–K summarize the coherence between the different component clusters through representation of their

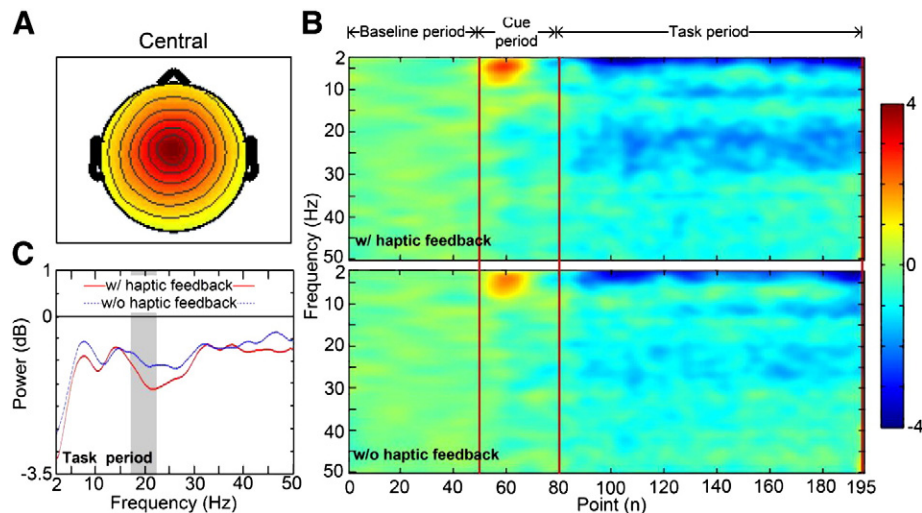


Fig. 5. The mean scalp maps, averaged group time–frequency responses and spectral changes of a central component cluster during a visuomotor tracking task.

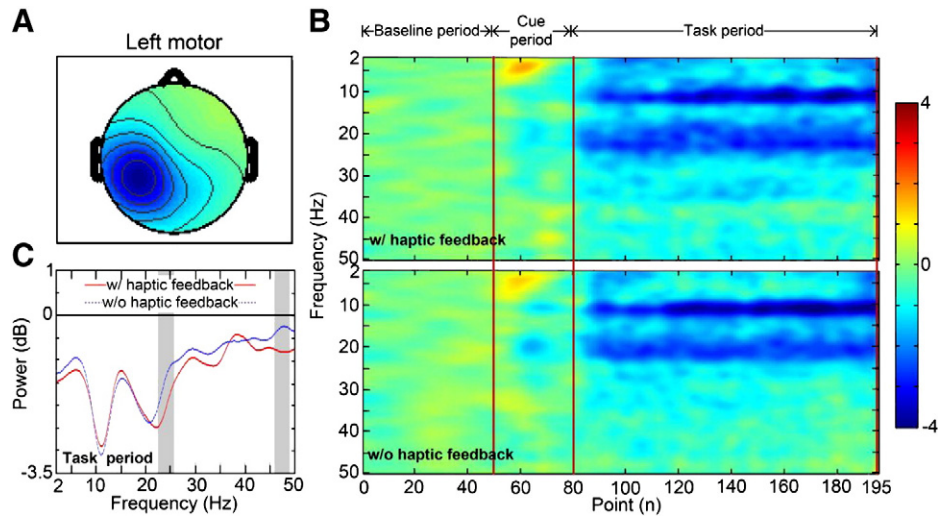


Fig. 6. The mean scalp maps, averaged group time–frequency responses and spectral changes of a left motor component cluster during a visuomotor tracking task.

scalp topographies, for which coherence values were significantly different between haptic and non-haptic feedback conditions under different frequency bands.

Discussion

Association of external stimuli with motor commands has proven helpful in enhancing the performance of motor learning (Maxwell et al., 2001; Schmidt and Wulf, 1997). External stimuli can be either visual, auditory or tactile (Deutsch et al., 2004; Lee et al., 1990; Lieberman and Breazeal, 2007; Merians et al., 2002; 2006; Millar and Al-Attar, 2004). However, in contrast to the present study, previous studies addressing motor learning tasks using EEG focused on visual and auditory signals to offer continuous guidance of motor commands (Blum, 2008; Blum et al., 2007, 2008). Until now, there has been no EEG study describing brain activity or reporting interactions between different brain regions during learning associated with haptic feedback. Therefore, this study was designed to investigate the differences in brain activities between visuomotor tracking in both the presence and absence of haptic guidance. The results of the current behavioral study showed that both the frequency of tracking errors and the number of adjustments during haptic feedback sessions were markedly reduced when compared to those that occurred without haptic feedback. This result suggests that haptic feedback can

improve motor learning (Fig. 2), which is consistent with the conclusions of prior behavioral studies (Lin et al., 2010; Morris et al., 2007).

The present study focused on two measurements of brain activities: the spectral power of components and the coherence between component activations. Measurement of coherence has been described in a variety of EEG studies, including investigations involving learning and motor tasks (Classen et al., 1998; Gruber and Muller, 2005; Miltner et al., 1999; Pollok et al., 2005; Serrien and Brown, 2003). Coherence was calculated based on intra-cerebral model signals, which provided direct information about the interrelationship of EEG signals (Lehmann et al., 2006). However, these previous studies utilized EEG signals recorded from the scalp to analyze the coherence between different brain activities. These analyses could have been confounded by the fact that scalp-recorded EEG signals report mixtures of activities from both brain and non-brain sources. Zervakis et al. (2011) indicated that the separation, identification and analysis of the independent activities of different brain areas are necessary in EEG analysis. To this end, component analysis has been widely used to separate EEG signals in accordance with the sensory, motor or cognitive functions of the brain (Lee et al., 2003; Zervakis et al., 2011). The present study employed independent component analysis (ICA) to decompose multi-channel EEG data into temporally independent components (Bell and Sejnowski, 1995; Makeig et al., 1997), which were then analyzed further via time–

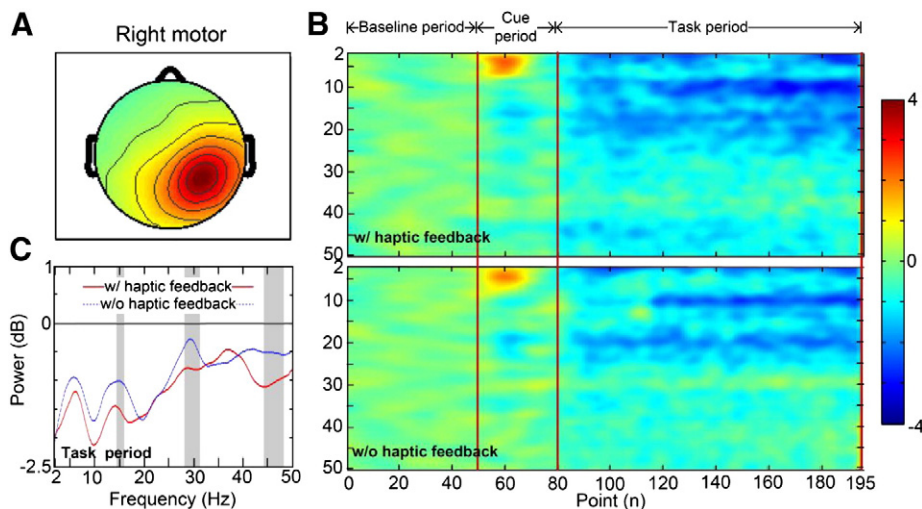


Fig. 7. The mean scalp maps, averaged group time–frequency responses and spectral changes of a right motor cluster during a visuomotor tracking task.

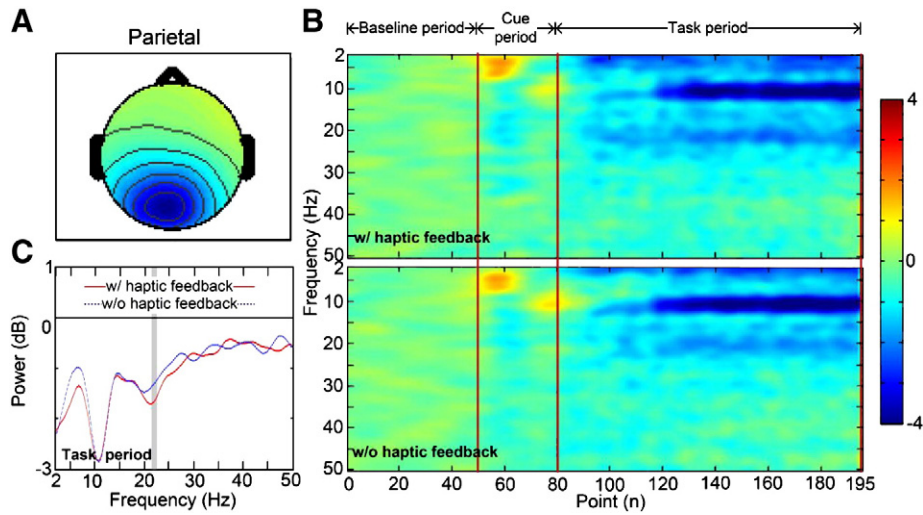


Fig. 8. The mean scalp maps, averaged group time–frequency responses and spectral changes of a parietal cluster during a visuomotor tracking task.

frequency analysis (event-related spectral perturbation or ERS, as described by Makeig, 1993) and event-related coherence (ERCOH; Babiloni et al., 2010; Vecchio et al., 2010) to determine brain activities during motor learning in the presence of haptic feedback.

This study demonstrates that haptic feedback facilitates the improvement of motor learning and provides evidence indicating that the obtained enhancements are accompanied by changes in ERSs and ERCOH. The following sections discuss the changes in the ERSs and ERCOH of component clusters under different task conditions.

EEG spectral changes associated with haptic and non-haptic feedback

ERSs are thought to reflect changes in the activities of local interactions between neurons and interneurons (Kranzloch et al., 2008). In this study, the changes in ERSs across all component clusters were grouped into three periods (i.e., baseline, cue and task periods). This study first tested that there was no significant spectral difference between epochs with and without haptic feedback during baseline periods. In the following sections, we discuss the changes in ERSs during the cue and task periods.

Cue period

The current study finds that the ERSs of seven component clusters (the medial frontal, left frontal, central, left motor, right motor,

parietal, left occipital and right occipital component clusters) exhibited a theta power increase that was time locked to the onset of cues relative to the ERSs of the baseline period. Following the theta-band increase, the ERSs of five clusters (the left motor, right motor, parietal, left occipital and right occipital component clusters) exhibited an alpha-power decrease. No significant spectral difference was observed between epochs with and without haptic feedback during the cue period. This result was not surprising because the experimental conditions were equivalent during the cue period for both epoch groups. Both pre-stimulus theta (particularly around the anterior region) and alpha (particularly around the posterior region) activities may reflect pre-stimulus top-down preparation for the performance of subsequent tasks (Min and Park, 2010).

Task periods

This study showed that the frequency of tracking errors and the number of adjustments in epochs with haptic feedback were lower than those in the absence of haptic feedback. During the task period, the ERSs of all eight component clusters exhibited delta-power suppression when compared to those of the baseline periods. Recent studies have suggested that it is reasonable to predict an association between changes in movement, speed and direction during learning and variations of low-frequency oscillatory activity (in the range of delta and low theta bands; <7 Hz) (Acharya et al., 2010; Waldert et

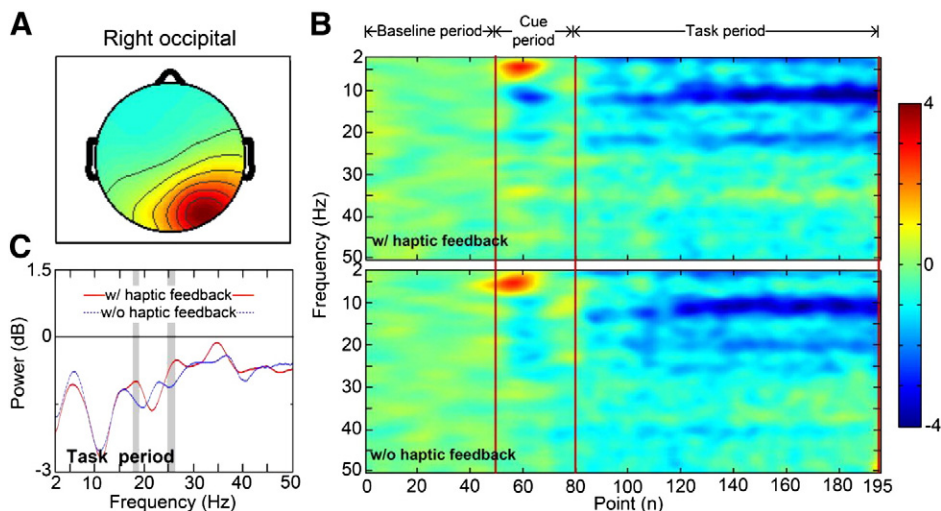


Fig. 9. The mean scalp maps, averaged group time–frequency responses and spectral changes of a right occipital cluster during a visuomotor tracking task.

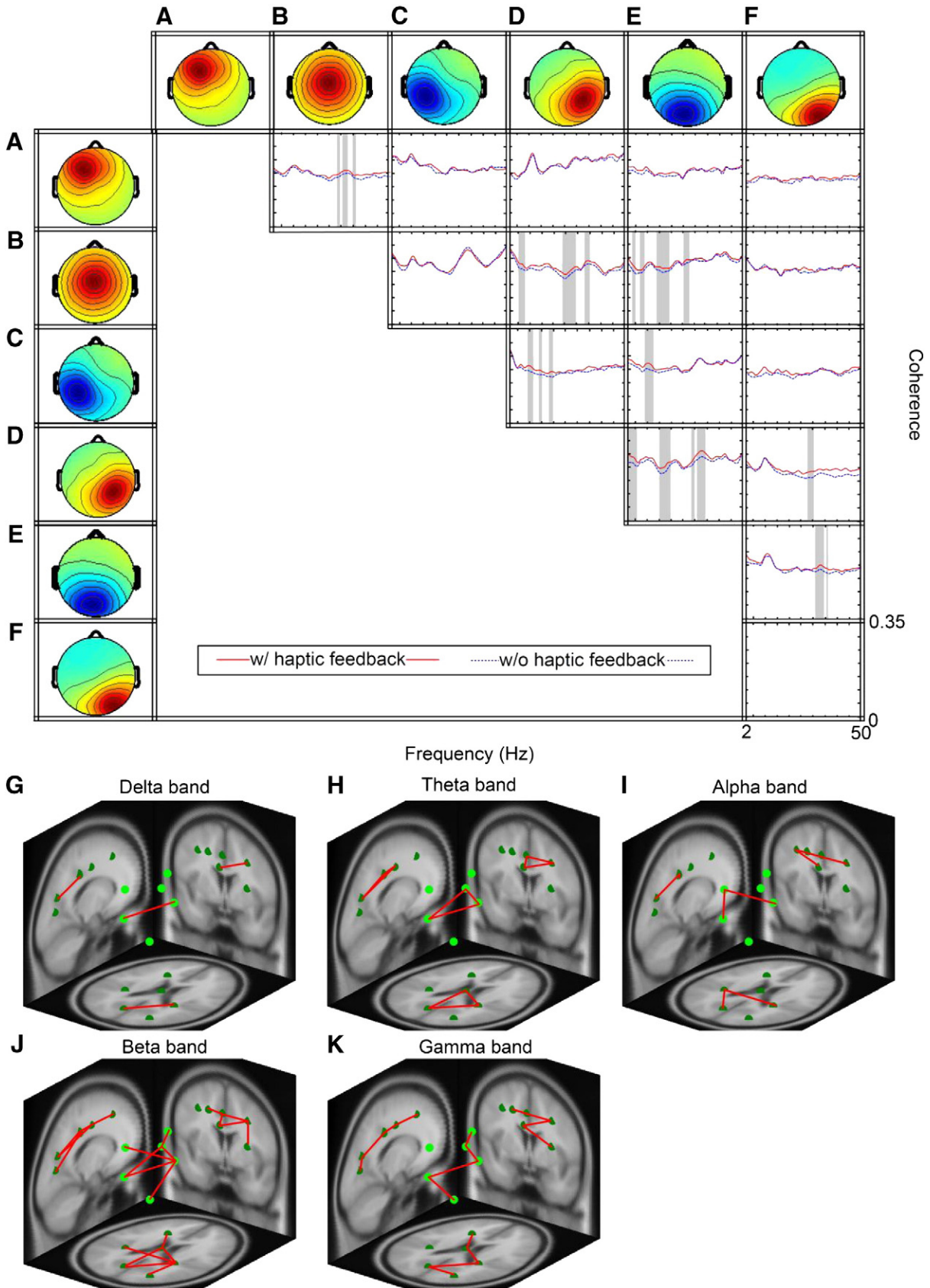


Fig. 10. ERCOH between different clusters for epochs with (solid red line) and without (dashed blue line) haptic feedback and interactions between component clusters under different frequency bands. (A–F) The gray bar indicates the frequency bins in which the coherence value differed significantly between haptic and non-haptic feedback conditions ($p < 0.05$; as determined by a paired-sample Wilcoxon signed-rank test). (G–K) Each sphere in the plot represents the location of the equivalent dipole for a component cluster. The red line between spheres represents the coherence between corresponding component clusters and is significantly different in epochs with and without haptic feedback.

al., 2008). In addition, the ERSPs of all eight component clusters exhibited decreases in alpha power and beta power relative to those recorded during the baseline period. Previous studies have suggested that several cortical areas may be involved in processing sensory or cognitive information or in the execution of motor behavior (Kruczoch et al., 2008; Pfurtscheller and Lopes da Silva, 1999). Furthermore, the ERSPs of all eight component clusters also exhibited gamma-power suppression compared to those observed in the baseline periods. Recent studies have suggested that initial visuomotor learning is associated with the enhancement of gamma power experienced during the execution of movement and that the changes in gamma bands co-vary with motor behaviors (Ng et al., 2011; Perfetti et al., 2011a).

The averaged PSD of the parietal, left frontal, central, left motor, right motor and right occipital component clusters exhibited statistically significant spectral differences between haptic and non-haptic conditions. In particular, the right motor displayed greater alpha-power suppression. The frontal, central, left motor, right motor and parietal component clusters exhibited greater beta-power suppression, and the left frontal, left motor and right motor clusters showed strong gamma-power suppression. In contrast, the right occipital component cluster exhibited reduced power suppression when subjects received haptic feedback (Figs. 4–9). It is noteworthy that statistically significant spectral differences between haptic and non-haptic feedback appeared most frequently in the beta band; this is consistent with the findings of previous studies that suggested that cortical beta amplitude is modulated by motor performance (Boonstra et al., 2007; Toma et al., 2002).

When tracking tasks are guided by continuous external information and haptic feedback, motor control requires ongoing processing and transformation of sensory information into motor commands. Therefore, there is ongoing distributed computation in the sensorimotor network involving the sensory, parietal, premotor and primary motor areas (Blum, 2008; Blum et al., 2008). In this study, the PSDs of six component clusters exhibited statistically significant spectral differences between the two conditions. In the following sections, we discuss the PSDs of these six component clusters under different frequency bands in detail.

Alpha band

Right motor clusters. The present study showed that the right motor component cluster exhibited larger alpha event-related desynchronization (ERD) for epochs with haptic feedback. The alpha-ERD during the observation or execution of action may reflect indirect modulation of motor activity in terms of mu-rhythm suppression by mirror neurons (Muthukumaraswamy and Johnson, 2004). Furthermore, Orgs et al. (2008) suggested that alpha-ERD was sensitive to the expertise of a certain movement repertoire, which supports the notion that the human observation–execution matching system is finely tuned to individual experience (Calvo-Merino et al., 2006). Moreover, alpha-ERD may serve as an indirect measure of the activity of such a system. Thus, the alpha-ERD result for the right motor component cluster indicated that haptic feedback can enhance the human observation–execution matching system as well as the planning and execution of hand movement. Conversely, the present study only showed significant differences in alpha ERD for the right motor component cluster between haptic and non-haptic feedback conditions. One possible explanation for this finding is that the observed difference in ipsilateral alpha activity between haptic and non-haptic feedback may only reflect co-contraction of the arm muscles (Novakovic and Sanguineti, 2011).

Beta band

Left frontal and parietal component clusters. Reed et al. (2005) showed that the inferior and superior parietal areas were activated during haptic object localization. Seitz et al. (1997) suggested that

kinematic representations of graph-motor trajectories are multiply represented in the parietal cortex. These studies indicated that different parietal sub-systems may sub-serve attentive sensory movement control and whole-field visuo-spatial processing. Furthermore, the parietal cortex is crucially involved in early stages of motor learning and motor adaptation, during which task execution strongly relies on external stimuli. This is because the involvement of the parietal cortex in early learning stages is attributed to the integration of external information into appropriate movement commands and to spatial processing (Doyon et al., 2003). Therefore, the difference in parietal spectral changes between epochs with and without haptic feedback may reflect the fact that haptic feedback was continuously delivered to the subjects and that task execution strongly relied on the haptic stimuli during the tracking task. In advanced stages of motor learning, the parietal and left frontal cortices are crucially involved in the storage of acquired skills (Halsband and Lange, 2006; Van Mier et al., 1998). Stoeckel et al. (2003) also reported that the left frontal and parietal cortices are activated for short-term storage of somatosensory information. In addition, activation of the frontal cortex is commonly reported during the initial stages of explicit motor learning (Doyon et al., 2003; Halsband and Lange, 2006). This is in accordance with the findings of an earlier study that suggested that the frontal cortex is involved in decision making, the selection of movements and attention processing (Deiber et al., 1997). In particular, the left frontal cortex appears to play a specific role in encoding during trial-and-error learning. Therefore, the involvement of the parietal and left frontal component clusters detected in present study suggests that haptic feedback could sub-serve motor learning and enhance the storage of somatosensory information during learning of motor skills. The parieto-frontal circuit, also known as the parieto-frontal mirror system, has been shown to play an important role in movement coding and action understanding (Fabbri-Destro and Rizzolatti, 2008; Hickok, 2009; Rizzolatti and Fabbri-Destro, 2008). In the present study, the improvement of behavioral performance (motor learning) facilitated by haptic feedback might be attributed to the involvement of this parieto-frontal mirror system, which was evident from the augmented beta-band power suppression in the participating brain regions.

Central and motor component clusters. Sensory processing or motor behavior leads to the desynchronization of central beta rhythms in EEG analyses, which reflects an amplitude decrease for cortical rhythms that occurs in response to external or internal events (Jasper and Penfield, 1949; Sochůrkova et al., 2006). In this study, the dipole model of the central component cluster was located near the medial motor area involving the cingulate cortex. The cingulate cortex is known to be involved in executive control, conflict monitoring, error detection, task evaluation and the execution of behavioral adjustments (Carter et al., 1998; Rushworth and Behrens, 2008). Furthermore, explicit motor learning is accompanied by an enhancement of beta power suppression over the medial motor area. Therefore, this area may play an integrative role in execution and on-line monitoring (Pfurtscheller and Neuper, 2010). The dipoles of the motor component clusters in the present study were localized in the primary motor area. The primary motor area is involved in early motor learning processes (Muellbacher et al., 2001) and the acquisition of motor skills (Gandolfo et al., 2000). Muellbacher et al. (2002) also reported that this area is crucial during early stages of motor memory consolidation. During explicit motor training, learning-related increases in activation have been shown to occur in the contralateral primary motor cortex (Van Mier et al., 1998). The present study clearly showed the involvement of the central, left and right motor component clusters in motor-tracking tasks, as epochs with haptic feedback exhibited stronger beta suppression than those without feedback. These differences could result from the fact that haptic feedback provides more explicit learning of movement and involves more sensory processing, on-line monitoring, acquisition of motor skills, and

consolidation of the early stages of motor memory than non-haptic feedback does.

Left and right occipital component clusters. The results of the present study demonstrate that both the left and right occipital component clusters were similarly activated during the course of the experiments. However, only the right occipital component cluster showed statistically significant differences in EEG beta-band power between epochs with haptic and non-haptic feedback. The occipital lobe includes the primary visual cortex, the lateral occipital region, MT complexes, fusiform gyri, and dorsal occipital–parietal regions (McAvoy et al., 2008). In the present study, the equivalent dipole model of the left occipital component cluster was located near the primary visual cortex, whereas an equivalent dipole model of the right occipital component cluster was located near the right-lateral occipital cortex. The primary visual cortex is where the earliest stage of visual processing occurs in the human cerebral cortex (Alink et al., 2010). In the left occipital component cluster, there was no significant change in the amount of activation associated with tasks with or without haptic feedback. This result was not unexpected because the visual stimuli were the same under both conditions. Visual–tactile convergence of object-related information occurs in the lateral occipital tactile–visual region (Amedi et al., 2001), which is a sub-region within the lateral occipital cortex. This part of the cortex is robustly activated during both visual and tactile object recognition, and both vision and touch share common representations (Easton et al., 1997; Reales and Ballesteros, 1999). This may explain why only the right occipital component cluster, which was localized at the lateral occipital cortex, showed statistically significant spectral differences between haptic and non-haptic feedback. James et al. (2002) reported observing activation in the lateral occipital cortex during haptic exploration of novel objects via functional magnetic resonance imaging (fMRI). These objects were used to reduce the potential influence of visual imagery. Therefore, we suspected that the haptic feedback design utilized in the present study might reduce the influence of visual imagery and improve visual presentation during the experiment.

Gamma band

Left frontal component clusters. Our experimental results demonstrate that the left frontal component cluster exhibited strong gamma power suppression for epochs with haptic feedback. Gamma-band decreases over the left frontal component cluster are enhanced during attentive periods (Sperduti et al., 2011). With a few notable exceptions (Hirata et al., 2004; Lachaux et al., 2008), gamma-band desynchronization has rarely been reported. Interestingly, all of the studies referenced above utilized written words or letters and concluded that left frontal gamma-band desynchronization was related to the translation of a cue letter (D or I) into the corresponding word (Duration or Intensity). Although these previous studies did not address motor skill learning, they suggested that gamma-band responses in the frontal cortex arrested upon conclusion of the cognitive process and were related to the successful processing of task-relevant information in short-term memory exercises (Rieder et al., 2011). Furthermore, gamma responses in the frontal cortex predicted successful encoding and better memory performance. Therefore, in this study, we speculated that haptic feedback could enhance cognitive processes and processing of task-relevant information, thereby improving motor performance.

Motor component clusters. Rhythmic activity carries information about sensory stimuli (Siegel et al., 2007), cognitive processes (Siegel et al., 2008), or motor acts (Miller et al., 2007). Specifically, limb movements are accompanied by suppression of low-gamma (<50 Hz) activity, which is typically stronger in the motor cortex (Donner et al., 2009). Donner et al. (2009) suggested that the gamma-band activity in the primary motor cortex during stimulus presentation might reflect local network interactions that help

maintain evolving motor planning. Furthermore, Huo et al. (2011) suggested that gamma oscillations in the primary motor cortex may reflect the activation of cortical–subcortical networks during the onset of discrete movements. Additionally, gamma oscillations may signal the direct modulation of outputs from the sub-thalamic nucleus to the basal ganglia, thereby facilitating the execution of movement. In the present study, the bilateral motor component clusters all exhibited strong gamma power suppression for epochs with haptic feedback. The results obtained for the bilateral primary motor seem to suggest that haptic feedback may help maintain an evolving motor plan and facilitate the execution of movement.

Interactions between different brain regions with haptic feedback

In analysis of coherence, it is generally assumed that coherent activity reflects an interaction between different brain areas involved in a particular task (Engel and Singer, 2001; Varela et al., 2001). In light of this widely accepted theory, Singer and Gray (1995) suggested that increased practice would enhance coherence between participating brain regions. Practicing a particular motor skill is necessary to attain expertise in that motor performance. This relationship is thought to be associated with changes in the strength of cooperation between different brain regions (Serrien and Brown, 2003). In addition, Serrien and Brown (2003) suggested that an increase in coherence between alpha and beta bands occurs when learning a new task, followed by a decrease when task performance improves. In the current study, haptic and non-haptic feedback epochs were extracted if their corresponding tracking errors were greater than 3 pixels. Therefore, because their performances were poor, we expected that the haptic and non-haptic feedback epochs corresponded to the early learning stage. Although the coherence between different component clusters among haptic and non-haptic feedback was generally comparable, there were relative increases in coherence for epochs with haptic feedback relative to those without haptic feedback.

Connections between different brain component clusters under different frequency bands appear to implicate different functions of the brain. The following section discusses the connections between different component clusters under different frequency bands.

Delta band

Parietal and right motor component clusters. Our results showed that delta-band coherence increased between the parietal and right motor cortex regions for epochs with haptic feedback compared to those without haptic feedback. Wymbs and Grafton (2009) suggested that during sequence execution for trials performed according to a random training schedule, brain activity significantly increases in a largely posterior cortical and cerebellar network, which included the ipsilateral primary motor cortex and parietal cortex. Perfetti et al. (2011a) demonstrated that significant local changes in delta activity were associated with learning that was localized in the parietal cortex. In addition, Chen et al. (1997) suggested that the ipsilateral primary motor cortex plays a specific role in voluntary movement. In associative tasks, delta oscillations in the primary motor cortex may act as an “internal metronome” related to the appearance of task-relevant cues, thereby performing a mechanistic role in the amplification of sensory inputs (Saleh et al., 2010). Our results are consistent with these reports in suggesting that haptic feedback can facilitate sequence execution, as the sensory inputs derived from haptic feedback in the present study are greater than those experienced without haptic feedback.

Theta band

Central, parietal and right motor component clusters. The present study showed that the ERCOH between the central region and two

additional ICs (the parietal and right motor) presented significant increases in the theta band for epochs with haptic feedback. Theta oscillatory activity is necessary for the maintenance and utilization of memory (Perfetti et al., 2011a). Therefore, increases in theta coherence indicate the formation of new internal models during visuomotor learning. In addition, Perfetti et al. (2011b) suggested that theta activity is required for formation of an accurate motor plan and is associated with enhancements of motor performance. Thus, we speculated that differences in theta-band coherence between haptic and non-haptic feedback conditions were linked to different motor memory formations. Furthermore, haptic feedback can influence motor learning by enhancing the accuracy and success of motor plan formation.

Alpha band

Left, right motor and parietal component clusters. During the execution of repetitive movements, it has been observed that there is greater alpha coherence between electrode sites overlying the bilateral sensorimotor and primary motor cortex, the supplementary motor area (SMA) and the posterior parietal cortex (PPC) (Holz et al., 2008). The present study showed that the alpha coherence between the billeted motor and parietal cortices presented a similar distribution to that described in this previous study (Holz et al., 2008). The previous study also suggested that brain activity in the alpha band is related to motoric activation. The experimental findings presented here showed that ERCOH between the left motor region and two additional ICs (the right motor and parietal regions) displayed significant increases in the alpha band for epochs with haptic feedback, suggesting that differences exist between motoric activation in the presence and absence of haptic feedback.

Beta band

In addition to the differences in component PSDs between haptic and non-haptic feedback, the present study demonstrates that the observed differences in coherence values between haptic and non-haptic feedback mostly occur in the beta band. It appears that the beta band plays a specific role during movement. Several studies have indicated a functional role for beta oscillations in sensorimotor behavior. For example, Classen et al. (1998) reported beta coherence between electrodes overlying visual and motor areas during a visuomotor tracking task. Some studies have found movement-related power and coherence changes in the beta band during the initial learning of a motor task (Mima et al., 2000; Serrien and Brown, 2002; 2003). Therefore, changes in the motor aspects of a task are mostly reflected in the beta band (Gerloff and Andres, 2002).

Frontal and central component clusters. The present study showed that relative increases in beta-band coherence between frontal and central cortex occurred for epochs with haptic feedback. Erla et al. (2011) found that execution of motor tasks induced activation in both frontal and central regions in the beta band; subsequently, these authors suggested that the role of this rhythm was associated with the feedback-mediated matching of visual information and motor performance. Thus, the present study suggests that differences in beta coherence between haptic and non-haptic conditions result from differences in feedback-mediated matching. Furthermore, haptic feedback can aid in matching visual information to motor performance.

Central and right motor component clusters. The present study detected increases in the coherence between central and right motor component clusters in epochs with haptic feedback relative to those without feedback. Previous studies have suggested that the central cortex and primary motor cortex are associated not only

with sensory processing and the acquisition of motor skill but also with learning-related increases in activation during explicit motor training (Gandolfo et al., 2000; Jasper and Penfield, 1949; Muellbacher et al., 2001, 2002; Pfurtscheller and Neuper, 2010; Van Mier et al., 1998). Therefore, we speculated that the haptic feedback supplied in this study could enhance sensory processing and the acquisition of motor skills, thereby enhancing the learning of movement and consolidating early stages of motor memory.

Central and parietal component clusters. In comparison with external haptic stimuli, self-generated stimulation (intrinsic feedback) leads to minimal activation of the somatosensory cortex, parietal region and cingulate cortices; this is in agreement with a reduction in the perceived intensity of the stimulation (Blakemore et al., 1998; Frith et al., 2000). These previous studies specifically indicated that external haptic stimuli can enhance the activation of related cortices because such stimuli enhance the perceived intensity of the stimulation. The results of the present study showed that beta-band coherence increases between the central and parietal component clusters in epochs with haptic feedback, which may be attributed to intensification of the simulation.

Left and right motor component clusters. Chen et al. (2010) suggested that the modulation of hand movements is associated with brain oscillations at different frequencies, such as beta rhythms in the brain areas (e.g., the bilateral primary motor cortex) being engaged by the performance of an action. Furthermore, transient increases in beta amplitude during tactile exploration might be related to certain forms of attention and beta oscillations increase in response to task-relevant instruction cues (Saleh et al., 2010). The present study showed that ERCOH between the left motor and right motor component clusters exhibited significant increases in the beta band for epochs with haptic feedback. Therefore, we suggest that the relative increase of beta coherence in epochs with haptic feedback could lead to two common interpretations of the functional relevance of beta oscillations. The first is that beta oscillations are involved in maintaining a stable posture via inhibiting movement (Saleh et al., 2010), and the second is that they are related to some aspects of movement planning or attention (Schwartz et al., 2005).

Right motor and parietal component clusters. This study found increases in coherence between the right motor and parietal component clusters in epochs with haptic feedback. Previous studies have suggested that coherent brain activity in motor-parietal networks reflects integrative sensorimotor behavior. Additionally, interaction between the parietal and motor cortices may be involved in the integration of spatial information and execution of movement (Blum et al., 2007; Classen et al., 1998). Furthermore, Blum et al. (2007) suggested that a synchrony exists between the parietal and the motor cortices that could be important for the successful execution of task-related movements. Thus, coherence increases between the right motor and parietal component clusters may reflect enhancements in integrative sensorimotor processes when the movements are guided by external haptic feedback.

Right motor and right occipital component clusters. Our results showed that the right motor and occipital component clusters exhibited relative increases in beta-band coherence for epochs with haptic feedback. In the sections above, we hypothesized that the haptic feedback design used in the present study might have reduced the influence of visual imagery and improved visual presentation during the course of the experiment because haptic feedback stimulated more explicit learning of a movement. In addition, haptic feedback could facilitate additional sensory processing, on-line monitoring, motor skill acquisition and consolidation of the early stages of motor memory.

Gamma band

Frontal, central, right motor, parietal and right occipital component clusters. Perfetti et al. (2011a) suggested that gamma enhancement would serve to form a new representation that once established, could be used to bias and shape an internal model to improve motor planning. Gamma phase coupling is associated with the encoding and retrieval of visual information. Furthermore, the formation of new motor memories is enhanced by increases in gamma phase coupling (Perfetti et al., 2011a). Our results showed that gamma-band coherence increased for the frontal, central, right motor, parietal and right occipital component clusters for epochs with haptic feedback. These cortices are often implicated as crucial nodes in multisensory integration, attention, and motor planning (Deiber et al., 1997; Huo et al., 2011; Perfetti et al., 2011a, 2011b; Rushworth and Behrens, 2008). Indeed, these processes are especially important in motor learning because the discrepancy between feedback and feed-forward information triggers the development of new internal models and must occur via synergy among multiple regions. In support of these conclusions, we suspect that during motor learning, haptic feedback can enhance the development of new internal models.

Conclusions

By combining independent component analysis, time–frequency analysis (event-related spectral perturbation, ERSP) and event-related coherence (e.g. ERCOH) analysis, the current study examined the changes in brain activity that occurred when visuomotor tracking tasks were performed in the presence or absence of haptic feedback. ICA was used to separate multi-channel EEG signals into independent brain processes. Each independent brain processes represents electrical neurophysiological activities from a tight cluster of neurons. Components with similar scalp topography, dipole locations and power spectra from multiple subjects were grouped into component clusters. Additionally, ERSP and ERCOH analyses were employed to contrast the brain dynamics within and between several independent brain processes during a tracking task performed either with or without haptic feedback. In summary, this study demonstrates that haptic feedback improves the behavioral performance and associates haptic feedback with motor learning by describing a variety of spectral changes in different brain processes and the interactions between them.

Acknowledgments

This work was supported, in part, by the Aiming for the Top university plan of National Chiao Tung University, Ministry of Education, and Taiwan. Further support came from the UST-UCSD International Center of Excellence in Advanced Bio-engineering, sponsored by the Taiwan National Science Council I-RiCE program under grant number NSC-100-2911-I-009-101 and the NSoC program under grant number NSC-100-2220-E-009-016 100N462. This research was also sponsored, in part, by the Army Research Office (under contract number W911NF-09-1-0510) Army Research Laboratory (under contract number W911NF-10-2-0022). The views and conclusions contained in this document are those of the authors and are not representative of the official policies, either expressed or implied, of the U.S. Army or the U.S. government. The U.S. government is authorized to reproduce and distribute reprints for government purposes notwithstanding any copyright notation herein.

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