RESEARCH ARTICLE

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Task-related power and coherence changes in neuromagnetic activity during visuomotor coordination

Abstract We analyzed a set of full-head (66 channels, CTF Inc.) magnetoencephalography (MEG) data recorded when 5 subjects performed rhythmic right index-finger flexion and extension movements on the beat (synchronization) or off the beat (syncopation) with a visual metronome at 1 Hz. Neuromagnetic activities in the alpha (8–14 Hz), beta (15–30 Hz) and gamma (30–50 Hz) ranges were shown to correlate with different aspects of the task. Specifically, we found that, compared with the control condition in which subjects only looked at the visual metronome without making any movement, all the movement conditions were accompanied by a decrease of power in the alpha range (8–14 Hz) in sensorimotor channels of both hemispheres, and an increase of coherence among a subset of these channels. The same comparison showed that power changes in the beta range differentiate task conditions by exhibiting power increases for synchronization and power decreases for syncopation. Changes in the gamma range power were found to be related to the kinematics of movement trajectories (flexion versus extension). These results suggest that three important cortical oscillations play different functional roles in a visuomotor timing task.

Keywords Neuromagnetic oscillations · Human sensorimotor integration · Movement coordination · Alpha, beta and gamma bands · Synchronization and syncopation · MEG power and coherence

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Introduction

Neuroelectric (EEG) and neuromagnetic (MEG) activity of the human brain is known to exhibit prominent oscillations in the alpha (8–14 Hz), beta (15–30 Hz) and gamma (30–50 Hz) frequency ranges. Recent work has shown that these oscillations are sensitive to both externally and internally generated events (Hari et al. 1997; MacKay 1997). In particular, EEG/MEG power is shown to decrease over activated cortical areas, a phenomenon termed event-related desynchronization (ERD), while the opposite phenomenon, called event-related synchronization (ERS), is observed over inactivated or idling areas (Pfurtscheller and Lopes da Silva 1999).

EEG/MEG power is hypothesized to measure the degree of neural synchrony (Hämäläinen et al. 1993; Nunez 1995) in a local cortical area. ERD/ERS of EEG/MEG power has been used as an index for assessing cortical engagement in a given event in a variety of experimental paradigms. For voluntary finger tapping, it has been shown that prior to movement onset, EEG/MEG activities were desynchronized in both alpha and beta ranges (Stancák Jr and Pfurtscheller 1996a; Rappelsberger et al. 1994; Leocani et al. 1997; Gerloff et al. 1998) in sensorimotor areas. While alpha oscillations maintained ERD throughout the task, beta activities exhibited ERS following the completion of the movement, signaling a postmovement rebound in beta power (Stancák Jr and Pfurtscheller 1996b). Involvement of gamma oscillations remains inconclusive in previous work (Pfurtscheller et al. 1993).

Whereas EEG/MEG power gauges neuronal interactions in a local cortical area, spectral coherence assesses functional coupling between distant areas of the brain. During discrete, self-paced finger movement, Rappelsberger et al. (1994) found coherence increases between central and frontal electrodes, and coherence decreases between central and temporal electrodes. Such event-related properties render coherence another cortical

functionality index complementing power spectra (Andrew and Pfurtscheller 1996).

Most ERD/ERS studies have focused on the phasic changes associated with simple discrete events. Steady state changes in power and coherence for sequential movements have been reported by Manganotti et al. (1998) and are referred to as task related power (TRPow) and task related coherence (TRCoh) changes. Specifically, Manganotti et al. observed that alpha and beta TRPow decreases were associated with TRCoh increases over frontocentral areas during movement preparation and execution. Classen et al. (1998) and Gerloff et al. (1998) employed more complex continuous sensorimotor tasks, and found that TRPow and TRCoh can be used to yield insight into the integration of visual and motor aspects of the tasks.

In this work we apply TRPow and TRCoh analysis to MEG recordings from a rhythmic sensorimotor coordination task. Subjects were required to perform anticipatory finger flexion or extension either in synchrony or by syncopating with a rhythmic metronome as whole-head MEG signals were recorded. The behavioral conditions were differentiated by task parameters such as movement direction, by different muscle group activations (extension and flexion), and by different timing requirements (synchronization and syncopation). Our goal was to identify the cortical dynamics associated with the different task components of these basic modes of coordination. Ensemble averaged data from the same experiment by Kelso et al. (1998) revealed a velocity effect that was independent of whether subjects performed synchronization or syncopation and flexion or extension. The analysis here, however, performed on the ongoing cortical activities, demonstrated that changes in brain oscillations are related to subtle differences in coordination behavior, which are not discriminated by traditional methods.

Previous behavioral studies of sensorimotor coordination have revealed that timing errors associated with periodically paced rhythmic movement are correlated as a $1/f^\alpha$ process (Chen et al. 1997, 2001). This means that human sensorimotor coordination evolves on multiple time scales. An associated finding is that distributed neural areas, including the cerebellum, sensorimotor cortex, supplementary motor area (SMA), superior temporal gyrus (STG), putamen and ventrolateral thalamus, are selectively engaged in tasks with different timing requirements (Harrington and Haaland 1999; Ivry et al. 1988; Rao et al. 1997). Here we investigate whether power and coherence methods can distinguish the neural networks and their temporal dynamics that underline different components of timing tasks.

Materials and methods

Experiment

The experimental protocol was approved by the local Institutional Review Board. Five right-handed subjects (three males and two
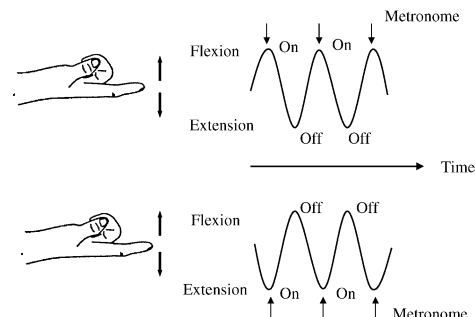

Fig. 1 A schematic representation of the four task conditions used in the experiment. Metronome onset is indicated as a *thin arrow*. *Sinusoidal curves* represent the ideal movement trajectories or the measured pressure profiles in extension and flexion directions. Notice that FON and EOFF though different tasks (synchronization and syncopation) may share similar movement trajectories. The same is true for FOFF and EON

females) gave informed consent and participated in the experiment. They were asked to flex or extend their right index finger to synchronize or syncopate with a visual metronome, delivered from a computer-controlled light-emitting diode (LED), placed 2 m away in front of the subject's central visual field. The subject's finger was placed between two inflated plastic pillows, each of which was connected to a pressure sensor by plastic tubing. The extensions and flexions were almost isometric and were recorded as the pressure changes on the two pillows. Each subject was required to perform four movement conditions: flexion on the beat (FON), extension on the beat (EON), flexion off the beat (FOFF) and extension off the beat (EOFF). A schematic representation of these four movement conditions is shown in Fig. 1. The control condition was a visual only (VO) condition in which subjects looked at the visual metronome without making any movement. For all the experimental conditions the visual metronome was set at 1 Hz. Each subject performed 100 cycles of movement for each condition and the movement conditions were randomized during the recording session.

The two "on" conditions (EON and FON) are synchronization tasks, while the two "off" conditions (EOFF and FOFF) are syncopation tasks. Based on the relative phase with respect to the metronome onset and the continuous nature of the movement, EON and FOFF conditions produce similar movement trajectories, because the extension phase of both EON and FOFF movements coincides with the onset of the metronome. The subject's intention and cognitive emphasis (to synchronize or to syncopate) is the key to differentiating the two conditions (Kelso et al. 1990). The same is true for EOFF and FON. So the four movement conditions can be grouped by movement direction (flexion or extension), task requirements (synchronization or syncopation) and different movement trajectories.

Experimental apparatus

Whole-head MEG data were recorded using an array of 66 SQuID (Super-conducting Quantum Interference Device) channels (CTF systems, Canada) covering both hemispheres of the brain. The channel locations are shown in Fig. 2. Visual inspections were performed to identify movement artifacts. Data from each channel were first low-pass filtered with the cutoff at 100 Hz, then notch-filtered at 60, 120 and 180 Hz to remove the effect of line frequency, and finally digitized at 250 Hz along with the metronome signal and the pressure-sensor voltages from the subject's movement response.
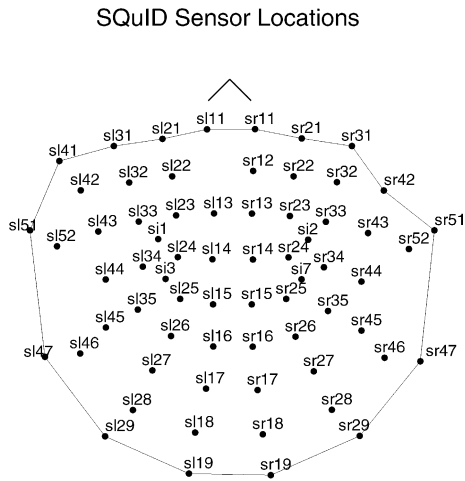
SQuID Sensor Locations

Fig. 2 Planar projection of the 3D SQuID recording system used to record human neuromagnetic activity in the brain. Sensor names and positions are shown. Subject is facing forward

Data analysis

For each of the five experimental conditions (VO, EON, EOFF, FON and FOFF), the 100-s continuous sweep of MEG data from each channel was linearly detrended and cut into 100 segments delineated by the stimulus onset. After deleting the first cycle to eliminate transients and rejecting cycles with artifacts, the remaining n cycles, where n is around 70 in each condition for all the subjects, comprised the ensemble of epochs for subsequent analysis.

Spectral power for channel i is computed according to:

$$\hat{S}_{ii}(f) = \frac{1}{n}\sum_{k=1}^{n} F(X_{ik} - \bar{X}_i)F(X_{ik} - \bar{X}_i)^* \tag{1}$$

where X_{ik} denotes the k-th epoch of the MEG data from channel i, $\bar{X}_i = \left(\sum_{k=1}^{n} X_{ik}\right)/n$ is the ensemble mean, $F()$ represents the Fourier transform and * stands for complex conjugate. Spectral coherence between channels i and j is defined as:

$$\hat{C}_{ij}(f) = \left|\frac{\hat{S}_{ij}(f)}{\sqrt{\hat{S}_{ii}(f)\hat{S}_{jj}(f)}}\right|^2$$

$$= \left|\frac{\sum_{k=1}^{n} F(X_{ik}-\bar{x}_i)F(X_{jk}-\bar{x}_j)^*/n}{\sqrt{\frac{1}{n}\sum_{k=1}^{n} F(X_{ik}-\bar{x}_i)F(X_{ik}-\bar{x}_j)^* \frac{1}{n}\sum_{k=1}^{n} F(X_{ik}-\bar{x}_j)F(X_{jk}-\bar{x}_j)^*}}\right|^2 \tag{2}$$

which can be interpreted as the cross-spectrum normalized by the power from both channels and has a value between 0 and 1.

When coherence $\hat{C}_{ij}(f)$ is significant between two channels at specific frequencies, the angle of the cross-spectrum $\hat{S}_{ij}(f)$, defined as

$$\hat{p}_{ij}(f) = \text{angle}\left(\hat{S}_{ij}(f)\right) \tag{3}$$

is the phase spectrum and can be used to provide information about the relative phase between channels i and j.

The above power and coherence calculation is based upon the assumption that the MEG data can be treated as approximately stationary across the whole epoch. This is partly supported by the fact that all the subjects maintained a stable response pattern by producing the required synchronization and syncopation conditions for each trial (see "Results"). This type of response was referred to as steady state response by Manganotti et al. (1998; see also Srinivasan et al. 1999). In addition, we directly examined the alpha,

beta, and gamma activities as a function of time within each epoch by band-pass filtering the MEG signal and performing an ensemble average of the resulting amplitude to obtain an amplitude profile for each frequency range. It was found that the amplitudes of the three oscillations were roughly constant within each cycle of the movement. This suggests that for the present experiment the processes underlying the MEG data can be considered stationary (Bendat and Piersol 1986) and can be subject to spectral analysis.

Statistical analysis of task-related power and coherence changes

In order to study task related changes, differences between the power and coherence from each movement condition and the VO condition were computed to form TRPow and TRCoh. To test whether the differences were statistically significant we first assess the variability of the estimators in Eqs. 1 and 2 by their standard deviations (Bendat and Piersol 1986):

$$\sigma_s(f) = \frac{1}{\sqrt{n}}\hat{S}_{ii}(f) \tag{4}$$

for power and

$$\sigma_c(f) = \frac{\left(2\hat{C}_{ij}(f)\right)^{1/2}\left(1 - \hat{C}_{ij}(f)\right)}{n} \tag{5}$$

for coherence. In both cases, n is the number of epochs in the ensemble, $\hat{S}_{ii}(f)$ and $\hat{C}_{ij}(f)$ are the estimated results from the data. Alpha (8–14 Hz), beta (15–20 Hz), and gamma (35–40 Hz) frequency bands were analyzed separately. The delimiters for the frequency bands were chosen based upon the observed strong power peaks across all the conditions and subjects (see "Results"). Within each frequency band, the coherence and power values were averaged across the frequency bins within the band before comparison. Significant changes in power and coherence were determined through a t-test using a Bonferroni-Dunn's multiple comparison correction. The overall significance level was chosen at $P<0.05$. This comparison was performed for each of the subjects individually and also on the grand average across subjects.

To test whether differences exist among the four movement conditions, a two-way ANOVA was performed on TRPow and TRCoh changes for the three distinct frequency bands. Post hoc pairwise comparisons for significant interactions were computed using the Tukey method of multiple comparisons (Glass and Hopkins 1984).

Results

Behavioral analysis

The relevant behavioral variable is the timing error, defined as the difference between the time of the appropriate extremum of the movement trajectory and the metronome onset (Kelso et al. 1998). All subjects performed the required coordination tasks well. The histograms (probability density functions) of the timing errors for the four movement conditions are plotted in Fig. 3 collapsed over the five subjects. Syncopation conditions (EOFF and FOFF) are more variable (larger errors as measured by the standard deviation) than synchronization conditions. This is expected because the syncopation tasks are more difficult to maintain, and appear to require more attention (Kelso et al. 1990; Carson et al. 1999; see also Temprado et al. 1999). In addition, the timing error distributions for the synchro-
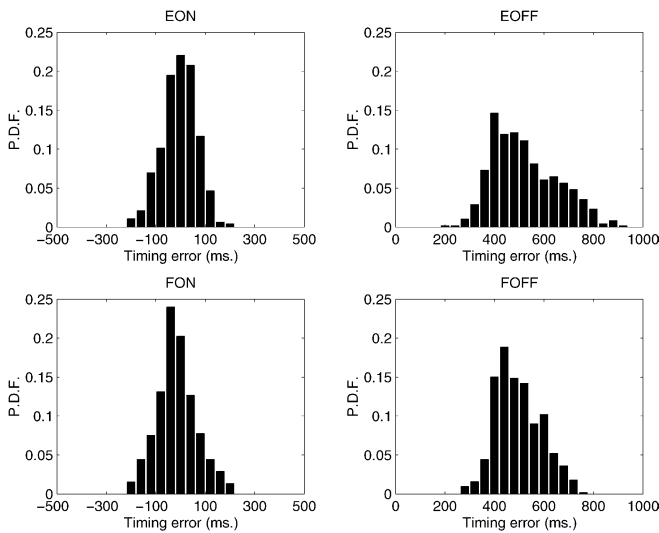
Fig. 5 Power spectra in units of pico Tessla squared (pT^2) from two sampled channels of one subject (WR). *Left figure* is from *si*3 in the left sensorimotor area, and the *right figure* is from *sl*18, left occipital area. Spectra for all the four experimental and visual only conditions are shown

Fig. 3 Histograms (probability density functions) of timing errors in the four movement conditions (modified from Fig. 1 in Kelso et al. 1998)
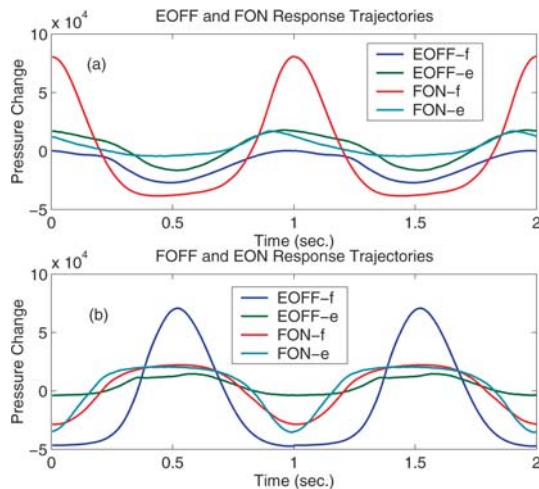

Fig. 4a, b Averaged behavioral response trajectories for the four movement conditions. To illustrate the periodicity of the movement trajectory, two stimulus cycles are plotted, corresponding to a 2-s time window, averaged with respect to the stimulus onset. Two pressure sensor recordings are shown in each condition. One sensor was on the flexion phase of the finger (e.g., EOFF-f); the other was on the extension direction of the finger (e.g., EOFF-e). It can be seen that the time courses of the trajectories are similar between EOFF and FON conditions (**a**), and between FOFF and EON (**b**)

nization conditions (EON and FON) are essentially symmetric, while the distributions for the syncopation conditions (EOFF and FOFF) are more skewed with long tails, suggesting an element of reaction to the stimulus. The movement trajectories for all four conditions, as measured by the finger pressure time series, are summarized in Fig. 4. As pointed out earlier, trajectories of EOFF and FON (top panel) are similar, while the same is true for FOFF and EON conditions (lower panel) (see also Fuchs et al. 2000). Our analysis of the cortical recordings
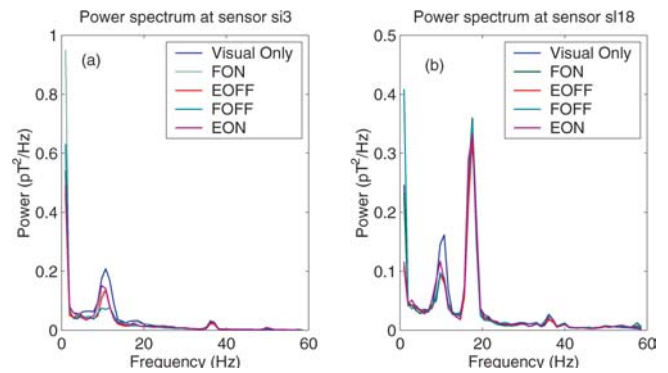
below examines the brain correlates of these behavioral differences.

Alpha (8–14 Hz), beta (15–20 Hz), and gamma (35–40 Hz) activity patterns revealed by power and coherence analysis

Oscillatory activities are identified by peaks in the power spectra. Figure 5 displays some representative examples from the left motor area (si3) and the left visual area (sl18) for all five experimental conditions. Peaks around the alpha (8–14 Hz), beta (15–20 Hz), and gamma ranges (35–40 Hz) are clearly seen. In addition, TRPow decreases in the alpha band for the movement conditions are readily visible. Similar results are obtained for all the data channels studied in this work. The frequency ranges identified here are also highly consistent with the published literature (Hari et al. 1997).

To evaluate the statistical interdependence among channels we computed the spectral coherence for all distinct channel pair combinations. Most of the coherence values are very low (close to 0), as seen in the coherence histogram (not shown) compiled for all subjects across all conditions, indicating independence among many channel pairs. Patterns of high coherence pairs yield clues to the formation of different networks. Following the terminology in McIntosh and Gonzalez-Lima (1994), we use the name network to refer to a collection of channels that exhibit high statistical interdependence. Figure 6 shows these networks for the three frequency bands for the Visual Only (VO) condition from all five subjects. Here only pairs with coherence in the top 5% are included in the plots. Threshold values are indicated below each plot.

For the alpha frequency band (8–14 Hz), shown in the top row of Fig. 6 for all five subjects, highly coherent groups of channels are seen in both hemispheres involving motor, frontal and parietal areas, and in occipital-temporal areas. Within each hemisphere, the phases among high coherence pairs are close to zero. Between

Fig. 6 Coherence patterns at alpha (8–14 Hz), beta (15–20 Hz) and gamma (35–40 Hz) frequency bands from all five subjects for the visual only (VO) condition. *Bottom color bar* represents the color coding of the coherence value (0–1). For each small figure, only the top 5% of coherence values are plotted. Threshold values are indicated below each plot
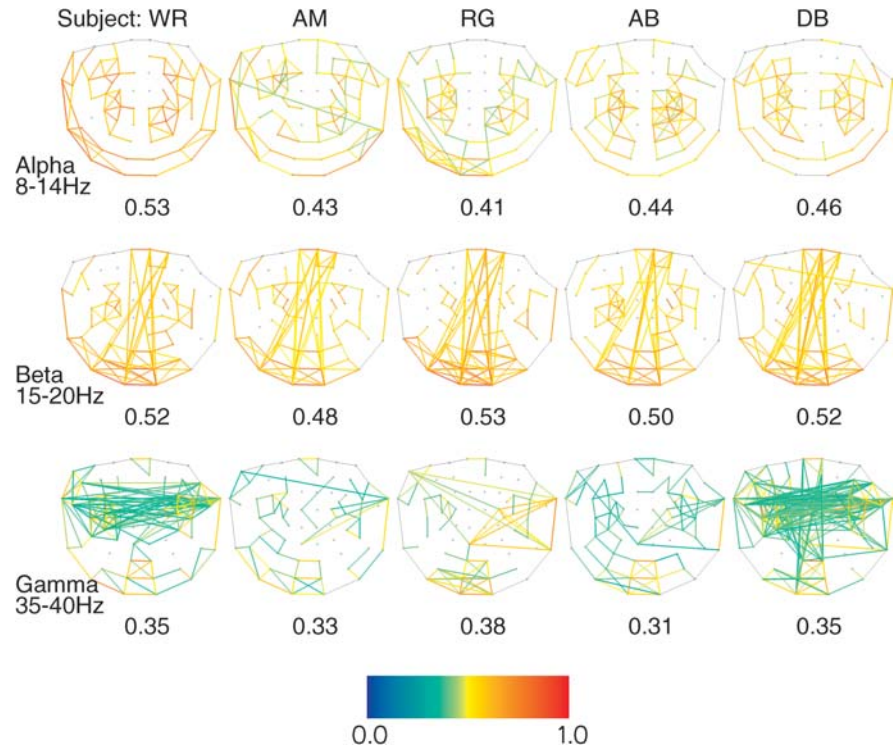
hemispheres, the coherence is low, a fact that is consistent with the characteristic rolandic mu rhythm (Salmelin and Hari 1994). The classical alpha activities formed a coherent group in the occipital-temporal area that is clearly separated from the mu networks.

For the beta band (15–20 Hz), shown in the middle row of Fig. 6, strong coherence exists between frontal and visual areas. For these strong coherent channels, we also calculated their relative phase through the phase spectrum defined in Eq. 3 (see data analysis in "Materials and methods"). While the relative phases within visual channels and within frontal channels are close to zero, these two areas are anti-phase to each other (relative phase close to π). There are also coherent activities within sensorimotor areas of each hemisphere. These patterns are consistent across all subjects.

For the gamma band (35–40 Hz), shown in the bottom row of Fig. 6, highly coherent networks are visible in two subjects (WR and DB). The involved sites are located in sensorimotor areas of both hemispheres. Intrahemispheric sites are in phase and interhemispheric sites are anti-phase with respect to each other. Some coherent activities between visual and frontal areas are also present but are more scattered.

The power and coherence patterns presented in Fig. 6 provide a basis upon which to compare all the task conditions. Significant changes are assumed to provide functionally relevant information in terms of specific attributes of the behavioral task.
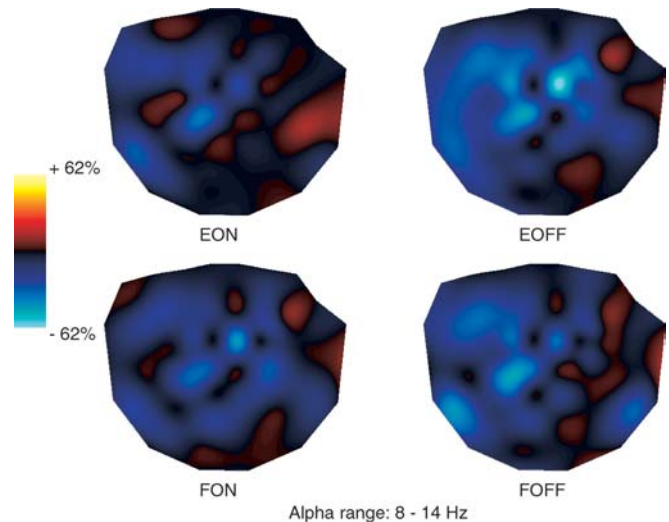

Fig. 7 TRPow changes in the alpha range (8–14 Hz) averaged across subjects. Each condition (EON, EOFF, FON, FOFF) was compared with the visual-only control condition. *Color bar* represents the coding of power changes. *Red* and *yellow* mean increases (Task-Related Synchronization); *blue* refers to power decreases (Task-Related Desynchronization). The *percentage values on the color bar* represent the maximal range of power changes in each condition

Alpha activities differentiate sensorimotor coordination from VO control condition

Statistically significant TRPow changes (in percentages), averaged across subjects, for the four movement conditions in the alpha band (8–14 Hz) are shown in Fig. 7.

Similar TRPow decreases in the motor areas of both hemispheres, especially on the contralateral side, for all movement conditions are seen. Moreover, EON and FOFF conditions share similar patterns in the detailed locations of the maximal TRPow changes, while FON and EOFF patterns are similar to each other. The amplitudes of TRPow changes in EOFF and FOFF conditions are slightly higher than FON and EON conditions, but the difference did not turn out to be significant. This TRPow decrease phenomenon is analogous to the mu rhythm ERD in self-paced movement (Stancák Jr and Pfurtscheller 1996a).

To test whether TRPow changes in the alpha range are different among the four movement conditions, a two-way ANOVA was performed, with movement conditions ($n=4$: EOFF, EON, FOFF, FON) and channel locations ($n=50$ excluding 16 channels with artifacts) as factors, and subjects ($n=5$) as repeated measures. This analysis showed that movement condition effects were not significant ($F_{(3,12)}=0.87$, $P<0.48$), but there were significant channel effects ($F_{(49,196)}=1.76$, $P<0.0038$) and a significant interaction ($F_{(147,588)}=1.54$, $P<0.0003$) between movement conditions and the channel locations. Post hoc Tukey tests revealed only three pairs of differences at two channel locations (see Table 2, left column), and failed to provide a consistent picture for the differences among the four movement conditions. This suggests that overall patterns of alpha desynchronization discriminated neither the specific types of the movement (Extension or Flexion) nor the task requirements (Synchronization or Syncopation).

Figure 8 shows the patterns of TRCoh changes. For reference we also plotted in the same figure significant TRPow changes as colored buttons at the individual channels. The channels with significant TRCoh changes were connected by lines where the magnitude of the changes was color coded. Two main features were seen in the TRCoh changes. First, the cross-hemisphere coherence increased in EON and FOFF conditions, and is absent in EOFF and FON conditions. This phenomenon seems to group the movement conditions according to the similarity of their trajectories. However, recalling that the
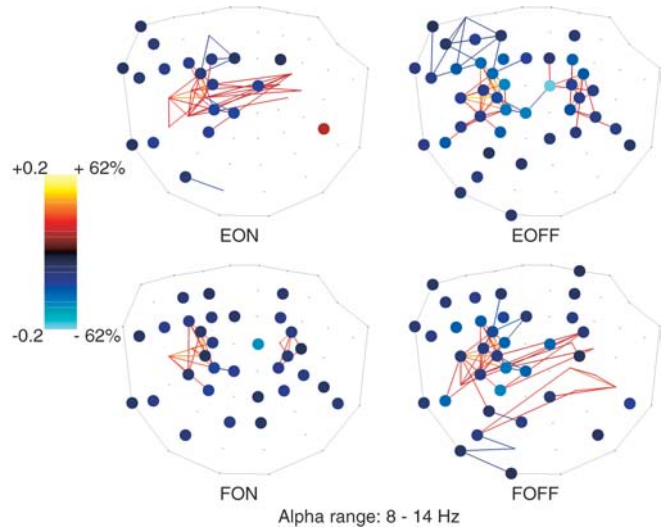

Fig. 8 TRPow and TRCoh changes in the alpha range (8–14 Hz). TRPow changes are represented as *colored dots* at each sensor location, where *blue* indicates power decreases and *yellow* means power increases. Significant TRCoh changes are represented as *color-coded lines between channels,* where *blue* refers to coherence decreases and *yellow* and *red* mean coherence increases. The *numbers on the color bar* refer to the maximal coherence and power changes within each condition

alpha range interhemispheric coherence is very low in the VO condition (Fig. 6), despite the significant increases seen in Fig. 8, the overall coherence values between hemispheres in EON and FOFF conditions remain small. The second phenomenon, which is consistent across all four movement conditions, is the significant TRCoh increases among a group of sensorimotor channels of both hemispheres, while the same channels showed TRPow decrease. The same patterns of TRPow and TRCoh changes were observed in all five subjects. Table 1 summarizes the intrahemispheric channel pairs that exhibited these patterns.

To examine the nature of these TRCoh changes, a representative coherence spectrum from one subject between the channel pair, si3 and sl34, in the left sensorimotor area is plotted in Figure 9. For the VO

Table 1 Intrahemispheric channel pairs showing coherence increases during movement conditions in the alpha range from a "decoherent" state during the visual only condition (see Fig. 8). For each subject, pairs from the left hemisphere and pairs from the right hemisphere are separated by ";"

| Subject	Channel pairs
Subject WR	si1-si3, si1-sl24, si1-sl25, si3-sl34, si3-sl44, sl23-sl24, sl24-sl33, sl24-sl34, sl24-sl44, sl25-sl34, sl25-sl44; si2-sr24, si2-si7, si2-sr35, sr24-sr33, sr24-sr34, sr25-sr34
Subject AM	si1-si3, si1-sl25, si1-sl34, si3-sl23, si3-sl24, si3-sl33, si3-sl34, si3-sl35, si3-sl44, sl24-sl25, sl24-sl34, sl25-sl34, sl34-sl35; si2-sr24, si2-si7, si7-sr25, si7-sr34, si7-sr35, sr24-sr34
Subject RG	si1-sl34, si3-sl24, sl43-sl44; si2-sr24, sr14-sr24, si7-sr25
Subject AB	si1-si3, si1-sl23, si-sl24, si1-sl33, si3-sl33, si3-sl34, si3-sl35, si3-sl44, sl23-sl43, sl24-sl33, sl24-sl44, sl25-sl44, sl33-sl34, sl33-sl35, sl33-sl43, sl34-sl43, sl34-sl44, sl35-sl44; si2-sr24, si2-sr25, si2-sr33, si2-sr34, si2-sr35, si7-sr33, sr25-sr33, sr33-sr34, sr33-sr35
Subject DB	si3-sl24, si3-sl25, si3-sl35; si2-sr33, sr23-sr33
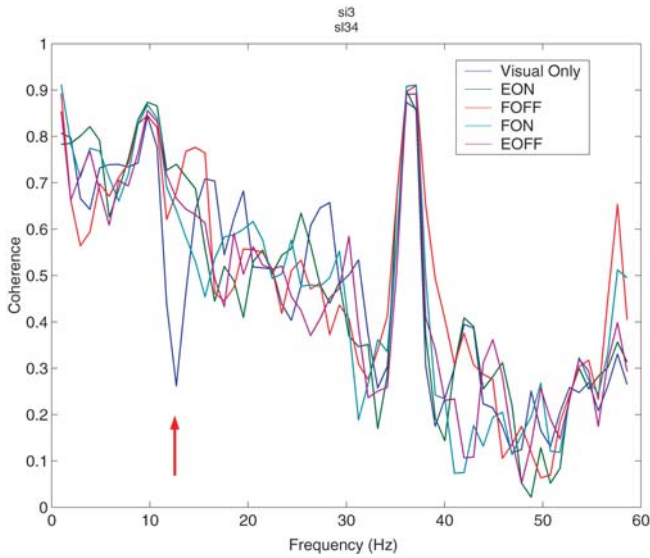
Fig. 9 An example of coherence increases across all frequency bands (0–60 Hz) from one subject. Shown is the coherence spectrum between channels *si*3 and *sl*34, both in the left sensorimotor area. Notice the clear low coherence values between 8 and 14 Hz in the Visual-Only condition and the strong coherence in gamma band in all five conditions

condition, even though these two channels are spatially very close, their coherence is very low in the alpha range (10–14 Hz), appearing as a sharp dip in an otherwise slowly changing coherence spectrum. For all four move-

ment conditions, however, this low coherence dip disappeared and the coherence spectra increases to a high level across a broad range of frequencies. Significantly, these changes of coherence were accompanied by TRPow decreases in the same channels, giving credence to the argument that neural components in the desynchronized local areas are engaged in a task-related manner.

Figure 10 illustrates significant TRPow and TRCoh changes in the alpha range for all five subjects across all coordination conditions. While the grand averages (last column) represent the most consistent effects across subjects, several individual differences are notable. For example, subject RG did not show power decreases in the 8- to 14-Hz range. Subjects RG and AB showed power and coherence increases in postparietal areas, which probably contributed to the increases of interhemisphere coherence observed in the grand average. Nevertheless, the most consistent phenomenon observed across subjects is the decrease of power and intrahemispheric increase of coherence in sensorimotor areas. This effect suggests that during the VO condition, sensorimotor neurons form segregated (desynchronized) groups that are locally synchronized in the 10- to 14-Hz range. During coordination conditions, levels of local synchronization are reduced, resulting in lowered power at the corresponding channels. In the meantime, the previously "decoherent" and segregated oscillatory neural groups become more synchronized, giving rise to higher values of interarea coherence. These changes of local and global synchronization patterns within and between sensorimotor loca-

Fig. 10 Individual TRPow and TRCoh changes for each subject across all coordination conditions and their averages in the alpha frequency range. *Blue* represents decreases in power and coherence; *yellow* and *red* refer to increases in power and coherence. *Numbers below each figure* are the individual maximal range of coherence and power (in percentage) changes
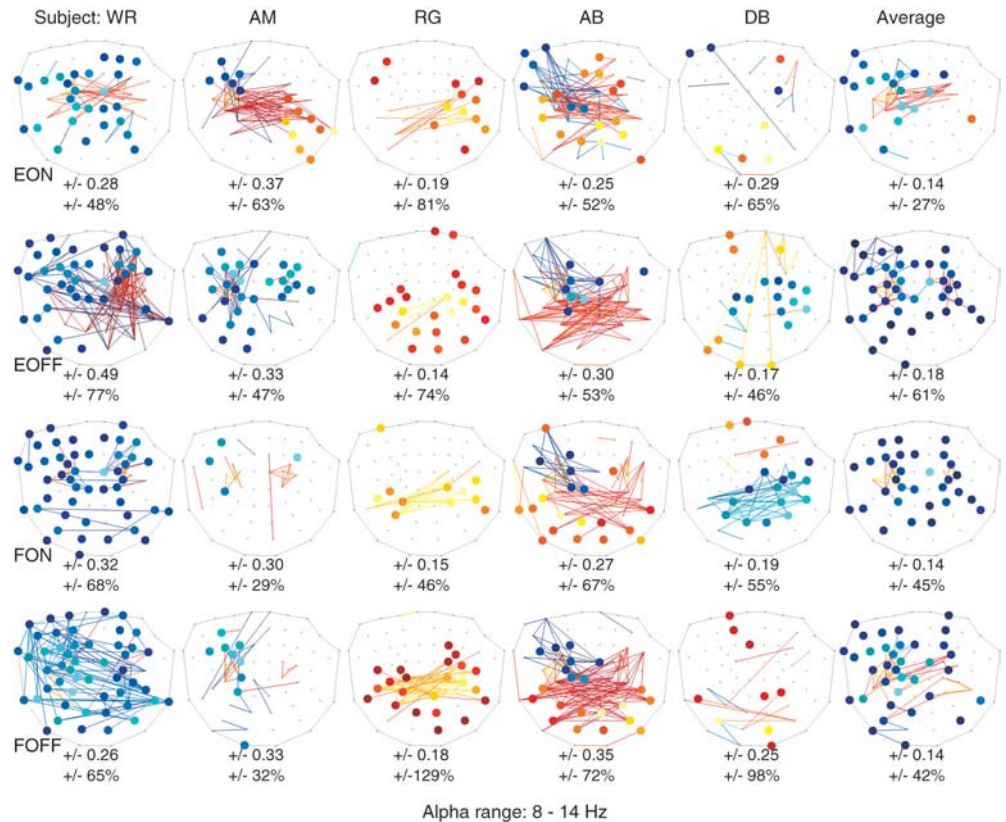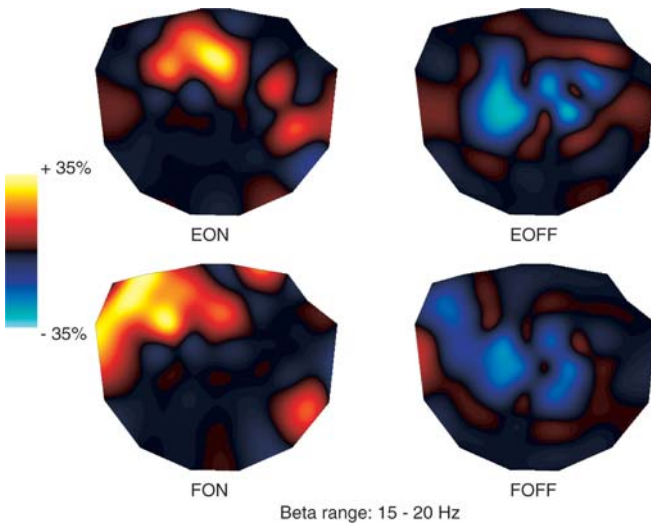
Fig. 11 TRPow changes in the beta range (15–20 Hz) averaged across subjects differentiate the synchronization conditions (EON and FON) from the syncopation conditions (EOFF and FOFF). Color bar represents the maximal range of power changes (in percent) in each condition

tions do not differentiate specific movement conditions. Rather, they discriminate "No-movement" from "Movement" conditions, suggesting that sensorimotor coordination involves the activation of a large-scale network.

Beta activities differentiate synchronization from syncopation

Figure 11 shows TRPow changes (grand averages) in the beta range (15–20 Hz) for all four coordination conditions. Clear TRPow increases are seen in the left sensorimotor and frontal areas (corresponding to Task-Related Synchronization) for the EON and FON coordination conditions, while the two syncopation conditions, EOFF and FOFF, exhibited TRPow decreases in senso-

rimotor and parietal areas (Task-Related Desynchronization). A two-way ANOVA was applied to TRPow changes in this frequency range (15–20 Hz), with movement conditions (n=4: EOFF, EON, FOFF, FON) and channel locations as factors, and subjects (n=5) as repeated measures. A movement condition effect ($F_{(3,12)}$=4.85, P<0.02) and a significant interaction between movement conditions and channel locations ($F_{(147,588)}$=1.99, P<0.0001) was present. Post hoc Tukey tests revealed 17 pairs of differences between conditions at 9 channel locations (see Table 2), involving left and right sensorimotor areas and left frontal areas. All the significant differences occur between "ON" (synchronization) and "OFF" (syncopation) conditions. No significant differences between the two synchronization conditions (e.g., EON and FON) or the two syncopation conditions (e.g., EOFF and FOFF) were found. This result suggests that task-related power changes in the beta range (15–20 Hz) differentiate synchronization and syncopation conditions, and are not related to movement directions (i.e., extension or flexion). Very few pairs showed significant TRCoh changes in this frequency range and they seemed to be randomly distributed (not shown). This means that functional coupling among distant cortical areas in the beta range is not task related (at least in the present context). Rather, the main task-related effect lies in the degree of synchrony within local areas.

Patterns of TRPow changes are meaningful in the context of known aspects of the behavior. The syncopation conditions (EOFF and FOFF) are an attention demanding, difficult task in which performance can be improved with learning (Jantzen et al. 2001). Beta range desynchronization correlates well with this aspect since beta oscillations are known to be activated by attentional demands (see also Jantzen et al. 2001; Mayville et al. 2001). On the other hand, if one hypothesizes that the encoding of time intervals involves frontal neurons, then the automaticity of the synchronization task (EON and FON) could make the time coding easier and reduce the

Table 2 TRPow comparisons among movement conditions. Condition pairs where post hoc Tukey methods of multiple comparisons revealed a significant difference in their respective TRPow and the corresponding channel are given for each frequency range. Recall that TRPow is defined as the power difference between a given movement condition and the visual only control condition (**P<0.01, *P<0.05)

| Alpha range (8–14 Hz)		Beta range (15–20 Hz)		Gamma range (35–40 Hz)	
Channel	Condition Pair	Channel	Condition Pair	Channel	Condition Pair
sr17*	FOFF FON	si1*	EOFF EON	sl28**	EOFF EON
sr26**	EON FON	si1**	EOFF FON	sl28**	EOFF FOFF
sr26**	FOFF FON	si1*	FOFF FON	sl28**	EON FON
		sl13**	EOFF EON	sl28**	FOFF FON
		sl13*	FOFF EON	sr18**	EOFF FOFF
		sl23*	EOFF EON	sr18**	FOFF FON
		sl23*	EOFF FON		
		sl25*	EOFF EON		
		sl33**	EOFF EON		
		sl33**	EOFF FON		
		sl42*	FOFF FON		
		sl42*	EOFF FON		
		sl42**	FOFF FON		
		sl43*	EOFF FON		
		sr14**	EOFF EON		
		sr14**	FOFF EON		
		sr25*	EOFF EON		
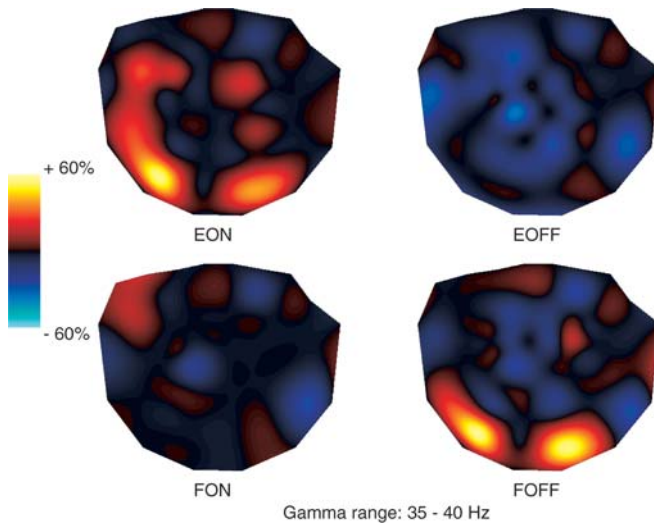
Fig. 12 TRPow changes in the gamma range (35–40 Hz), averaged across subjects. TRPow changes for EON and FOFF are very similar, both showing increases in left and right visual areas, while EOFF and FON are similar. Color bar represents the maximal range of power changes (in percent) in each condition

need for the active engagement of relevant neuronal groups, leading to a more idle (synchronized) frontal cortex.

Gamma activity differentiates movement trajectories

Figure 12 shows how TRPow changes in the gamma range (35–40 Hz) with task conditions. For the EON and FOFF conditions, TRPow in visual areas of both hemispheres increased, while in EOFF and FON conditions the task-related power mainly decreased. A two-way ANOVA with movement conditions and channel locations as factors showed significant condition effects ($F_{(3,12)}$=3.67, P<0.04). Post hoc Tukey tests revealed six pairs of significant differences between conditions (see Table 2), involving two channels in the left and right visual areas (*sl*28 and *sr*18). The pairs of differences seem to group EON and FOFF conditions together, and EOFF and FON together. As described earlier, these two groups of movement conditions are differentiated by their movement trajectories; that is, their spatial-temporal relation with respect to the external metronome. The reason visual areas are involved in discriminating movement conditions may lie in the interaction between motor and visual areas in achieving the required visual-motor coordination. Significant TRCoh changes in this frequency range were few and did not reveal any consistent pattern.

Discussion

Task-related power and coherence measures of brain activity can discriminate task components not seen by traditional average evoked responses. The present anal-

ysis also suggested differential functional roles of the alpha (8–14 Hz), beta (15–20 Hz) and gamma (35–40 Hz) band activities in a simple visuomotor coordination task. In particular, TRPow and TRCoh changes in the alpha range showed primarily movement effects, and did not differentiate specific aspects of the task. TRPow changes in the beta range were shown to be linked to task requirements and task difficulty, whereas gamma TRPow changes discriminated movement trajectories. Previous work (Salmelin et al. 1995) reported functional roles of 10- and 20-Hz activities in a discrete flexion movement. Our results here are consistent with this finding and provide a functional segregation of three brain oscillations during more complex forms of sensorimotor coordination.

Alpha activity reflects motor engagement
and possibly sensorimotor integration

A number of theories and models have suggested that occipital alpha activities are generated by the thalamo-cortical loop (Jahnsen and Llinas 1984a, 1984b). During strong alpha oscillations, the population of thalamocortical relay cells (TRCs) is hyperpolarized, thereby blocking the flow of information between cortex and subcortical structures, resulting in an "idling" of the involved cortical areas (Steriade et al. 1990). When alpha oscillations are suppressed (desynchronized), TRCs are less polarized and ready to mediate information transfer among brain areas. Although the exact mechanism of more anterior and more motor related alpha (mu) rhythm remains unclear, we think that a similar process might underlie the task-related desynchronization observed here. Event- or Task-Related Desynchronization in the alpha band in sensorimotor areas may indicate the transition of the cortical area from an "inactive" to "active" state, implying that a "gate" is opened for information processing involving sensorimotor cortex, thalamus, and subcortical structures controlling limb movements. As suggested by our experiment, this process may not be related to the details of the information being processed, such as the direction and velocity of the movement, the muscles involved or task requirements (see Kelso et al. 1998). Rather, alpha activity seems to be an indicator of the general state of large-scale sensorimotor activation.

The very low coherence between sensorimotor channels observed in the visual only condition suggests the presence of segregated idling alpha oscillations within sensorimotor areas. We interpret this finding in terms of the separation of sensory and motor activities when there is no movement. Behavioral studies (Aschersleben and Prinz 1995) have shown that, in order to maintain a required coordination pattern in the present experiment, subjects combine intended motor signals with tactile and proprioceptive feedback to produce movements at specific time relations with respect to the external metronome. We speculate that the disappearance of the "decoherent" state and the synchronization of previously independent alpha band activities reflects the integration

and binding of sensory and motor information during sensorimotor coordination.

It is generally believed that for EEG and MEG recordings, sensors that are physically close tend to have high coherence because they pick up activities from the same source. This problem is particularly severe for EEG because of the added factor of scalp volume conduction. Thus, some researchers chose to look only at coherence among channels separated by large distances (e.g., >12 cm in Srinivasan et al. 1999). Examples from the present research seem to contradict this view. In Fig. 9, the generally high values of coherence across a wide range of frequencies (especially below 30 Hz) can be attributed to common signals in these two nearby channels. However, significantly low coherences in a specific frequency range are not easily explained by the common source theory. In addition, the method used here in which coherence originating from non task-related sources in nearby channels is removed by the subtraction process, renders our coherence analysis applicable to any channel pairs regardless of the distance separating them. More importantly, the patterns of coherence changes during the task further suggest that coherence among close channels can be a genuine and meaningful indicator of neural functions. The present experimental design and analysis methods were able to pick up the few pairs of such interesting coupling in a vast number (>2000) of possible pairwise interrelations.

Functions of beta and gamma activities

Recent work on experiments similar to the one studied here revealed different attentional demands (Temprado et al. 1999) for anti-phase and in-phase coordinations. (These two conditions can be considered the bimanual analogue of the present syncopation and synchronization conditions.) Specifically, when the experimenters asked the subjects to react to a second task while performing in-phase or anti-phase bimanual coordination, the reaction time during anti-phase coordination (similar to syncopation) was significantly longer than during in-phase movement, suggesting greater allocation of attentional resources to the anti-phase mode than to the in-phase mode. Analysis here shows that patterns of TRPow changes in the beta range (15–20 Hz) are different between synchronization and syncopation tasks (see also Jantzen et al. 2001; Mayville et al. 2001). We suggest that these differences may be interpreted in terms of the cognitive differences that exist between synchronization and syncopation (Chen et al. 2001). In particular, the desynchronization of the beta band over parietal areas during syncopation signifies the increased engagement of underlying neural populations. This result is consistent with animal research suggesting that beta activities are related to attention. Murthy and Fetz (1992) found that there was more fast beta band (25–35 Hz) activity when monkeys performed a difficult, more demanding task than a simple repetitive task. Nashmi et al. (1994) found

similar increases in the power of EEG at 30–50 Hz when human subjects performed motor tasks with focused attention. These two examples were mainly in the higher beta range, not in the lower beta range (15–20 Hz) studied here, a fact that may contribute to the different directions of power changes associated with attention (see Mayville et al. (2001) for another possible explanation of the direction of power changes in terms of the spatial scales underlying different neural signals).

Most studies of beta oscillations find a relation to movement execution. For example, Kristeva-Feige et al. (1993) reported 18–19 Hz neuromagnetic activity related to a premovement wait (or idling) period. In EEG studies of brisk and discrete finger movements, Stancák and Pfurtscheller (1996b) found decreases of power (ERD) in the beta range before the movement, and a quick recovery and increase of power above baseline (ERS) after the execution of the movement. Salmelin et al. (1995) suggested that this rebound of beta power may be a signature of "active immobilization following movement." In these studies, the effect of attention has not been addressed. Instead, changes of power in the beta range (ERD before the movement and ERS after the movement) appear more related to the time course of the movement. From this perspective, the present results enrich our understanding of beta activity by relating it to different attentional demands between synchronization and syncopation.

Functions of TRPow changes in the gamma range are less clear in our experiment. As mentioned before, only two subjects showed systematic TRPow changes in our experiment, and the TRPow changes in Fig. 12 mostly represent the average of these two subjects. Because a visual metronome was used in the experiment, it is worth noting that the visual areas of both hemispheres showed strong ERS. Experimental conditions differentiated by the gamma activities are more related to the specific spatial-temporal relation between the movement profile and the timing of the external visual metronome, as shown in Fig. 1.

Conclusion

Recent studies of rhythmic timing experiments both at the behavioral level (Chen et al. 2001) and at the neurophysiological level (Mayville et al. 2002; Rao et al. 1997) suggest the involvement of distributed neural systems acting on multiple time scales. The present analysis of task-related power and coherence of signals from large-scale SQuID arrays reveals relations between neural oscillations and various aspects of the rhythmic timing task. In particular, alpha activity is found to be related to two possible functions, one reflecting the general activation of the motor system and the other serving to bind sensory and motor information. Beta activity is found to be related to task difficulty, differentiating synchronization from syncopation. It is further hypothesized that the beta activity changes reflect differential attentional

requirements. To give this idea sufficient credence future work that includes independent measures and manipulations of attention (e.g., probe RTs) is required. Finally, contrary to commonly held beliefs, high-frequency gamma band activity does not seem to be related to the binding or coordination of sensory and motor signals in the present task context. Instead, it discriminates differences in the actual movement trajectories. These results lead to the hypothesis that brain oscillations at three different frequency ranges might have different functional roles in the sensorimotor task studied here. Taken together with the previous analysis of averaged event-related neuromagnetic fields (Kelso et al. 1998), the present results provide a broader, yet more detailed picture of sensorimotor coordination and open up a number of future lines of investigation, including attention and learning, using these methods. Moreover, it will be a challenge now to incorporate the present results into theoretical models of the neural dynamics underlying this class of tasks (Jirsa et al. 1998; Fuchs et al. 2000; Jirsa and Kelso 2000; Kelso et al. 1998) that are based on established cellular and neural ensemble properties of the cerebral cortex.

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