

Neural correlates of regional EEG power change

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Received 3 August 2005; revised 1 April 2007; accepted 7 April 2007
Available online 25 April 2007

To clarify the physiological significance of task-related change of the regional electroencephalogram (EEG) rhythm, we quantitatively evaluated the correlation between regional cerebral blood flow (rCBF) and EEG power. Eight subjects underwent H₂¹⁵O positron emission tomography scans simultaneously with EEG recording during the following tasks: rest condition with eyes closed and open, self-paced movements of the right and left thumb and right ankle. EEG signals were recorded from the occipital and bilateral sensorimotor areas. Cortical activation associated with EEG rhythm generation was studied by the correlation between rCBF and EEG power. There were significant negative correlations between the sensorimotor EEG rhythm at 10–20 Hz on each side and the ipsilateral sensorimotor rCBF and between the occipital EEG rhythm at 10–20 Hz and the occipital rCBF. The occipital EEG rhythm showed a positive correlation with the bilateral medial prefrontal rCBF, while the right sensorimotor EEG rhythm showed a positive correlation with the left prefrontal rCBF. In conclusion, decrease in the regional EEG rhythm at 10–20 Hz might represent the neuronal activation of the cortex underlying the electrodes, at least for the visual and sensorimotor areas. The neural network including the prefrontal cortex could play an important role to generate the EEG rhythm.

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Keywords: Neural networks; Positron emission tomography (PET); Regional cerebral blood flow; Sensorimotor; Visual

Abbreviations: ANCOVA, analysis of covariance; EEG, electroencephalogram; EMG, electromyogram; EOG, electro-oculogram; ERD, event-related desynchronization; ERS, event-related synchronization; FWHM, full width at half-maximum; M1, primary motor cortex; PET, positron emission tomography; rCBF, regional cerebral blood flow; S1, primary sensory cortex; SM1, primary sensorimotor cortex; SPM, statistical parametric map.

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Available online on ScienceDirect (www.sciencedirect.com).

Introduction

The electroencephalogram (EEG) represents the summed postsynaptic potentials of cortical neurons (Niedermeyer and Lopes da Silva, 1987). The generator mechanisms of EEG rhythm in various frequency bands, however, are not well understood.

In normal subjects, the EEG rhythm at 8–12 Hz is usually most conspicuous over the parieto-occipital area (Berger, 1929; Pfurtscheller and Lopes da Silva, 1999) and is called the occipital alpha band rhythm. The EEG alpha band rhythm may be associated with the alert and yet relaxed state and is commonly used as an indirect measure of the functional organization of brain. It is well known that normal awake alpha band rhythms are ‘blocked’ (substantially reduced in amplitude) by eye opening and moderate to difficult mental tasks (Berger, 1930, 1932; Nunez et al., 2001; Vijn et al., 1991). Thus, some authors suggested that the occipital alpha band rhythm might be considered as an idling rhythm of visual areas (Kuhlman, 1978).

One of the most relevant activities overlapping the occipital alpha band rhythm is the so-called mu rhythm which is restricted over the hand area of the primary sensorimotor cortex (SM1) and is suppressed not by eye opening but by active hand movements. The sensorimotor mu rhythm could also be considered as an idling rhythm of sensorimotor areas (Kuhlman, 1978; Pfurtscheller, 1992). Although the role of the thalamocortical circuitry in the generation of sleep spindles has been emphasized (Steriade et al., 1990), the neurophysiological mechanisms by which the regional alpha band rhythm such as the occipital alpha or the sensorimotor mu rhythm are to be generated or suppressed are still unclear.

Higher frequency EEG waves such as the beta band rhythm (13–30 Hz) are associated with the cortical activation most pronounced during the awake state and rapid eye movement sleep (Nofzinger et al., 2000). During various motor tasks, EEG studies showed a transient decrease of EEG power in the beta band (Pfurtscheller, 1989), which is called event-related desynchronization (ERD) (Pfurtscheller, 1977; Pfurtscheller and Aranibar, 1977)

or task-related power decrease (Gerloff et al., 1998). This decrease starts 1–2 s prior to the movement onset and is followed by a rebound-like increase just after termination of the movement (event-related synchronization: ERS) (Pfurtscheller, 1992). It is speculated that the motor cortex shifts from an activated state during preparation and execution of movement (working cortex) to a resting state after termination of movement or, in other words, from a processing mode to an ‘idling’ mode (Pfurtscheller et al., 1996). This hypothesis is also supported by a transcranial magnetic stimulation study showing decreased corticospinal excitability at the time of the 20-Hz event-related synchronization (Chen et al., 1998). However, the generator mechanism of regional beta band rhythm is still unknown.

Brain electrical activity represents the single greatest demand on cerebral metabolism (Erecinska and Silver, 1989), suggesting that measurement of electrical energy also should be coupled to cerebral metabolism and perfusion. In normal subjects, cerebral glucose uptake and blood flow are generally accepted as tightly coupled measures of cerebral energy utilization (Sokoloff, 1977, 1981). The association between EEG power and cerebral glucose metabolism has been occasionally studied using the 18-fluoro-deoxyglucose positron emission tomography (PET) technique (Larson et al., 1998; Oakes et al., 2004; Schreckenberger et al., 2004). However, a limitation of the 18-fluoro-deoxyglucose tracer is that over the span of 30 min it is difficult to ensure that the subject remains in the same functional state (Oakes et al., 2004). Regional cerebral blood flow (rCBF) has been used as an indirect measure of functional neural activity (Raichle, 1987) and the PET technique is considered to be the ‘gold standard’ in CBF measurements in humans (Feng et al., 2004). Measurement of rCBF using $H_2^{15}O$ PET has been well established based on the single-tissue compartment model for diffusible tracers in at least physiologically normal brain tissue (Sadato et al., 1998). The $H_2^{15}O$ tracer has shorter time frame (10–30 s) than the 18-fluoro-deoxyglucose tracer (20–30 min) and the results of $H_2^{15}O$ PET examinations directly depend on the acute cerebral state of activation during tracer injection (Schreckenberger et al., 2004). In normal subjects, cerebral blood flow is generally accepted as tightly coupled measures of cerebral energy utilization (Sokoloff, 1977, 1981). It was reported that EEG power showed strong associations with rCBF in most frequency bands including the alpha and beta range (Leuchter et al., 1999). Therefore, taken together with the EEG power change described above, it is predicted that rCBF associated with the neuronal activation might covary with the EEG power in at least normal subjects. Although previous reports (Ingvar et al., 1976; Paulson and Sharbrough, 1974) mentioned the relationship between EEG and rCBF in humans, the record of EEG and rCBF could not be done simultaneously due to limitations in the EEG and rCBF technique. Recently, the association between EEG power and rCBF recorded simultaneously has been occasionally studied using the $H_2^{15}O$ technique (Leuchter et al., 1999; Nakamura et al., 1999; Sadato et al., 1998). However, the previous reports investigated a correlation between rCBF and the EEG rhythm averaged across the whole scalp. The averaged EEG rhythm might be inappropriate to investigate regional EEG power change such as sensorimotor mu rhythm because the occipital alpha band rhythm may diminish an effect of sensorimotor mu rhythm in the averaged alpha power. Therefore, it would be preferable to investigate the relationship between rCBF change induced by several tasks and the regional EEG rhythm to clarify

neurophysiological mechanisms in the generation or suppression of the regional EEG power. To achieve this goal, we employed rather simple tasks that are commonly used in clinical EEG recording.

The purpose of the present study is to quantitatively evaluate the correlation between rCBF changes using $H_2^{15}O$ PET and EEG power changes induced by several motor tasks and clarify what brain regions are involved in the generation and suppression of the regional EEG rhythms.

Methods

Subjects

Eight right-handed healthy volunteers (5 males and 3 females; mean age \pm SD, 42 \pm 10 years) participated in the experiment. The protocol was approved by the NINDS Institutional Review Board and the NIH Radiation Safety Committee. All subjects gave their written informed consent for the study and had no medical history of neurological or psychiatric disorders.

Tasks

The subjects lay in a supine position and the following tasks were performed twice for each (total 10 times):

1. rest condition with eyes closed (EC)
2. rest condition with eyes open (EO)
3. self-paced right thumb abduction and adduction movement (1–2 Hz) with eyes closed (RH)
4. self-paced left thumb abduction and adduction movement (1–2 Hz) with eyes closed (LH)
5. self-paced right ankle extension and flexion movement (1–2 Hz) with eyes closed (RF)

The order of tasks was randomized across subjects. Electrophysiological recording and PET scanning were carried out simultaneously in all conditions (Fig. 1).

Electrophysiological recording

EEG signals were recorded from 6 electrodes (O1, O2, C3, C4, FC3, FC4 according to the International 10–20 System) secured with collodion and referenced to the right earlobe electrode (A2). The left earlobe electrode (A1) was recorded as a separate channel. To reliably estimate the scalp EEG potential, we converted the EEG signals into the digitally linked earlobe reference before further analysis (Mima and Hallett, 1999; Nunez et al., 1997). A previous study showed that the electrode locations of FC3/C3, FC4/C4 and O1/O2 are just over the left and right SM1 and the occipital cortex, respectively (Steinmetz et al., 1989). Electromyogram (EMG) signals were recorded from 5 muscles (right abductor pollicis brevis [APB], biceps [BIC], left APB, BIC and right hamstring). To monitor the eye movement and blinking, electro-oculograms (EOGs) were monitored by pairs of electrodes placed at the left and right lateral canthus for horizontal eye movement and by another pair of electrodes placed below and above the right eye for vertical eye movement. To monitor tongue movement, a surface electrode placed at the upper edge of the right nasolabial fold

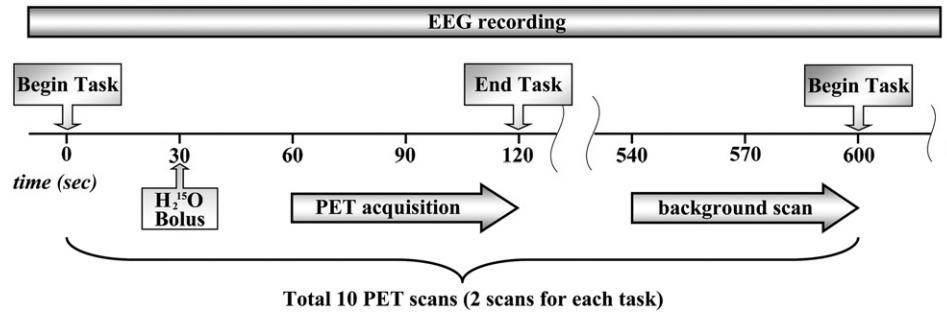


Fig. 1. Sequence and time course of the EEG/PET/task protocol.

and referenced to linked earlobe electrodes was used to record the glossokinetic potential. Impedance was kept below 5 k Ω . EEG and EMG signals were amplified and filtered by bandpass of 1–50 Hz and 10–50 Hz, respectively, and both were digitized at 250 Hz (Neuroscan, Neuroscan Inc. Herndon, VA). EEG and EMG signals during both conditions were segmented into non-overlapping and artifact-free epochs of 1024 ms which allowed a 1-Hz frequency resolution after Fourier transformation. Epochs with unwanted muscle activity were excluded from the analysis. Power spectra were computed by a fast Fourier transform algorithm implemented on the Neuroscan software. Based on the previous studies (Andres et al., 1999; Mima et al., 2000), the power spectra were grouped into four different frequency bands, 8–12 Hz (alpha), 13–20 Hz (beta1), 21–30 Hz (beta2), and 31–50 Hz (gamma). Since the high and low alpha band rhythms (Klimesch, 1999) behaved quite similarly in our experiment using the simple tasks, we analyzed the whole alpha band as one group. Although the gamma band activity is of special importance for cognition (Rodriguez et al., 1999; Tallon-Baudry and Bertrand, 1999), we did not analyze the gamma band activity because of the environmental electromagnetic noise in the PET scanning room and the possible contamination of EMG. In addition to the 60 Hz noise, the possible contamination of the muscle activity to the occipital electrodes because of the increased neck muscle tone was inevitable due to the tight head fixation for the PET scanning in a few subjects. The local EEG power was calculated by the averaging the EEG powers at 2 electrodes (FC3/C3, FC4/C4, and O1/O2) that were obtained during the PET procedure (60 s). A logarithmic transformation was applied to normalize the power (Halliday et al., 1995).

PET acquisition

$H_2^{15}O$ PET scans were obtained in 3D mode using a GE Advance PET tomograph (GE Medical System, Milwaukee, WI) with an axial field of view of 15.3 cm. The task performance began 30 s before bolus infusion of 10 mCi of $H_2^{15}O$ (half life 2.1 min) via a catheter in the left cubital vein. Scanning was started when a rising brain radioactivity count was first detected (20–30 s) after injecting the radio-isotope. Scanning continued for 60 s thereafter. Inter-scan interval was 10 min. A transmission scan obtained prior to each session was used to correct for attenuation. Head movement was minimized by using a thermoplastic mask that was molded to each subject's head and attached to the scanner bed. Each subject underwent 10

consecutive PET scans (2 scans for each task). The sequence and time course of the PET/EEG/task protocol are shown in Fig. 1.

Data analysis

The attenuation-corrected emission scans were reconstructed into 35 trans-axial planes, 4.25 mm apart, with an in-plane center resolution of 6.5 mm full width at half-maximum (FWHM) in each direction. Scans from each subject were realigned to correct the head motion during the study then normalized to a standard bicommissural stereotactic space (using Montreal Neurological Institute template) and smoothed with an isotropic Gaussian filter of 12 mm using SPM2 (Wellcome Department of Cognitive Neurology, London, UK) implemented in Matlab (Friston et al., 1990, 1991, 1995). After correction for variations in global blood flow (normalized to 50 ml/100 g/min) using analysis of covariance (ANCOVA), the multi-subject, covariate only design matrix was specified and the subjects with logarithmic EEG power during each task as a covariate were estimated according to the general linear model at each and every voxel, assuming a linear relationship between rCBF and the covariate. Both positive and negative correlations at each voxel were estimated for the occipital, left sensorimotor, and right sensorimotor EEG power. Therefore, the EEG bands of alpha, beta1, and beta2 were adopted in the right and left sensorimotor and occipital regions and a total of 9 covariates were included in separate design matrices. The occipital EEG power was also considered in both sensorimotor EEG power analyses as a nuisance factor because the occipital alpha and beta EEG could have an influence on the sensorimotor EEG.

The resulting whole brain statistical parametric maps of t -statistic (SPM(t)) had a final spatial resolution of 12.6 \times 13.7 \times 15.0 mm FWHM. The SPM(t) map was transformed into units of normal distribution (SPM(z)), where the significance of each region was estimated with a threshold of uncorrected $p < 0.001$. This uncorrected threshold is commonly used in SPM (Benoit et al., 2002; Salmon et al., 2000; Staff et al., 2000). Because of a large number of statistical comparisons in this voxel-by-voxel analysis, the Bonferroni correction was done to eliminate the probability of a type-I error. Because the Bonferroni correction is the most conservative correction for multiple comparisons and might result in a type-II error, statistical parametric maps that survived a threshold of $p < 0.001$ uncorrected for multiple comparisons were also shown. A higher threshold presented by a corrected $p < 0.05$ at cluster levels was also applied in order to

exclude the clusters that have any probability of being randomly produced (Bench et al., 1992; Salmon et al., 2000; Staff et al., 2000). The SPM coordinates for standard brain from Montreal Neurological Institute were converted to Talairach coordinates (Talairach and Tournoux, 1988) by a non-linear transform method (see <http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml>).

Results

The mean movement frequencies during the tasks (task 3, 4 and 5) were 1.3 ± 0.3 Hz in RH, 1.2 ± 0.2 Hz in LH and 1.3 ± 0.3 Hz in RF (no significant differences). The mean EEG alpha frequencies were 9.8 ± 0.9 Hz in the occipital area, 10.8 ± 2.1 Hz in the left sensorimotor area and 11.0 ± 1.5 Hz in the right sensorimotor area (no significant differences). The logarithmic regional EEG band power is shown in Fig. 2.

Brain regions correlated with the occipital EEG power

A significant negative correlation between the occipital alpha power and rCBF was found in the bilateral occipital cortices including the primary and association visual cortex (Fig. 3A, Table 1A). Similarly a negative correlation between the occipital beta1 power and rCBF was found in the bilateral occipital cortices (Fig. 3B, Table 1A). A significant negative correlation

between the occipital beta2 power and rCBF was found in the posterior part of the right middle temporal gyrus (Fig. 3C, Table 1A). A significant positive correlation between the occipital alpha power and rCBF was found in both lateral and medial prefrontal cortices and basal forebrain mainly on the left. The left superior temporal gyrus also showed a positive correlation (Fig. 3A, Table 1B). A significant positive correlation between the occipital beta1 power and rCBF was also found in both lateral and medial prefrontal cortices and the left superior temporal gyrus (Fig. 3B, Table 1B). No significant positive correlation was found between the occipital beta2 power and rCBF was found (Fig. 3C, Table 1B).

Brain regions correlated with the left sensorimotor EEG power

A significant negative correlation between the left sensorimotor alpha power and rCBF was found in the left pre- and postcentral gyrus and the left inferior parietal lobule (Fig. 4A, Table 2A). A significant negative correlation between the left sensorimotor beta1 power and rCBF was also found in the left pre- and postcentral gyrus (Fig. 4B, Table 2A). A significant negative correlation between the left sensorimotor beta2 power and rCBF was found in the left postcentral gyrus and inferior parietal lobule (Fig. 4C, Table 2A). No significant positive correlation between the left sensorimotor EEG power and rCBF was found (Figs. 4A–C, Table 2B).

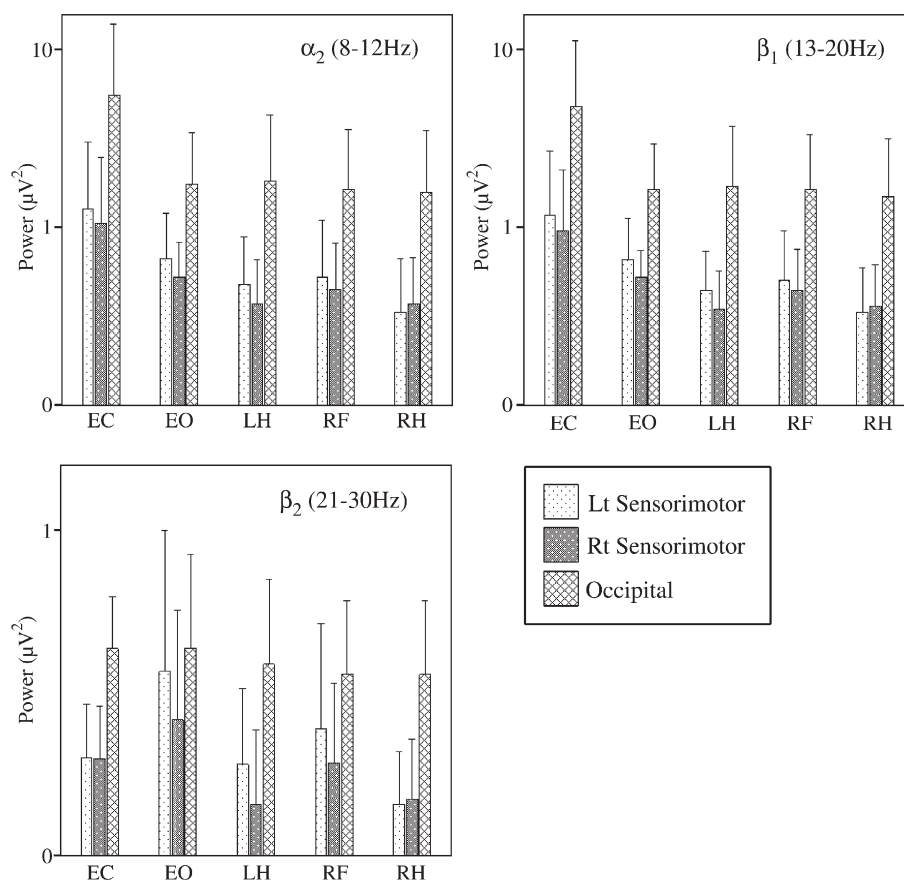


Fig. 2. Plot (mean values+standard deviation) of absolute regional EEG band power. EC, eyes closed; EO, eyes open; LH, left thumb movement; RH, right thumb movement; RF, right foot movement.

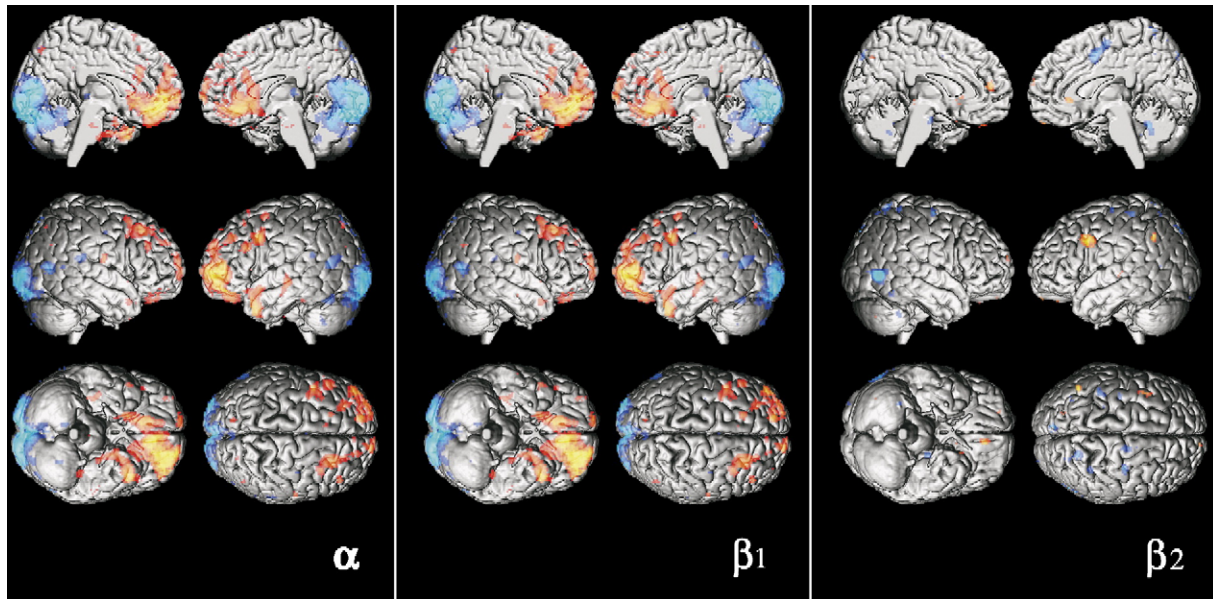


Fig. 3. Statistical parametric maps of positive (yellow-red) and negative (aqua-blue) correlation between rCBF and occipital EEG alpha, beta1 and beta2 power during each task, superimposed on surface-rendered MRI. Areas that survived a statistical threshold of $p < 0.001$ uncorrected for multiple comparisons are shown. A significant negative correlation between the occipital alpha and beta1 power and rCBF was found in the bilateral occipital cortices. A significant positive correlation between the occipital alpha and beta1 power and rCBF was also found in both lateral and medial prefrontal cortices.

Brain regions correlated with the right sensorimotor EEG power

A significant negative correlation between the right sensorimotor alpha power and rCBF was found in the right postcentral gyrus and inferior parietal lobule (Fig. 5A, Table 3A). A significant negative

correlation between each of the right sensorimotor beta1 and beta2 power and rCBF was also found in the right postcentral gyrus and inferior parietal lobule (Figs. 5B–C, Table 3A). A significant positive correlation between the right sensorimotor alpha power and rCBF was found in the left middle frontal gyrus (Fig. 5A, Table 3B).

Table 1
Brain regions (A) negatively and (B) positively correlated with the occipital EEG power

EEG band	Region	BA	Coordinate Talairach space			Cluster-level corrected P	kE	z
			x	y	z			
<i>(A) Negative correlation</i>								
Alpha	Rt lingual gyrus (GL)	19	20	-78	-11	0.000	9807	5.49
	Rt cuneus	18	10	-101	9			5.35
	Lt lingual gyrus (GL)	18	-8	-80	-13			5.29
	Lt fusiform gyrus (GF)	19	-22	-53	-11	0.003	456	5.10
Beta1	Rt lingual gyrus (GL)	19	20	-11	-11	0.000	9278	5.33
	Lt lingual gyrus (GL)	18	-8	-80	-13			5.16
	Rt cuneus	18	10	-101	9			5.12
	Lt fusiform gyrus (GF)	19	-24	-53	-12	0.006	398	4.99
Beta2	Rt middle temporal gyrus (GTm)	37	50	-62	3	0.011	358	4.10
<i>(B) Positive correlation</i>								
Alpha	Lt anterior cingulate	32	-8	44	-9	0.000	6018	5.27
	Lt superior temporal gyrus (GTs)	38	-49	22	-18	0.000	882	4.60
	Lt precentral gyrus (GPrC)	9	-38	13	34	0.025	289	4.34
	Lt middle frontal gyrus (GFm)	8	-46	10	42			3.62
	Rt middle frontal gyrus (GFm)	8	30	31	43	0.006	399	4.23
Beta1	Rt anterior cingulate	32	12	29	-6	0.000	5714	5.30
	Lt anterior cingulate	32	-8	44	-7			5.16
	Lt superior temporal gyrus (GTs)	38	-49	22	-18	0.000	703	4.39
	Rt middle frontal gyrus (GFm)	8	32	31	41	0.002	507	4.20
	Rt superior frontal gyrus (GFs)	8	40	20	51			3.65
Beta2	No suprathreshold clusters							

Clusters that survived a statistical threshold of $p < 0.05$ corrected for multiple comparisons are shown.

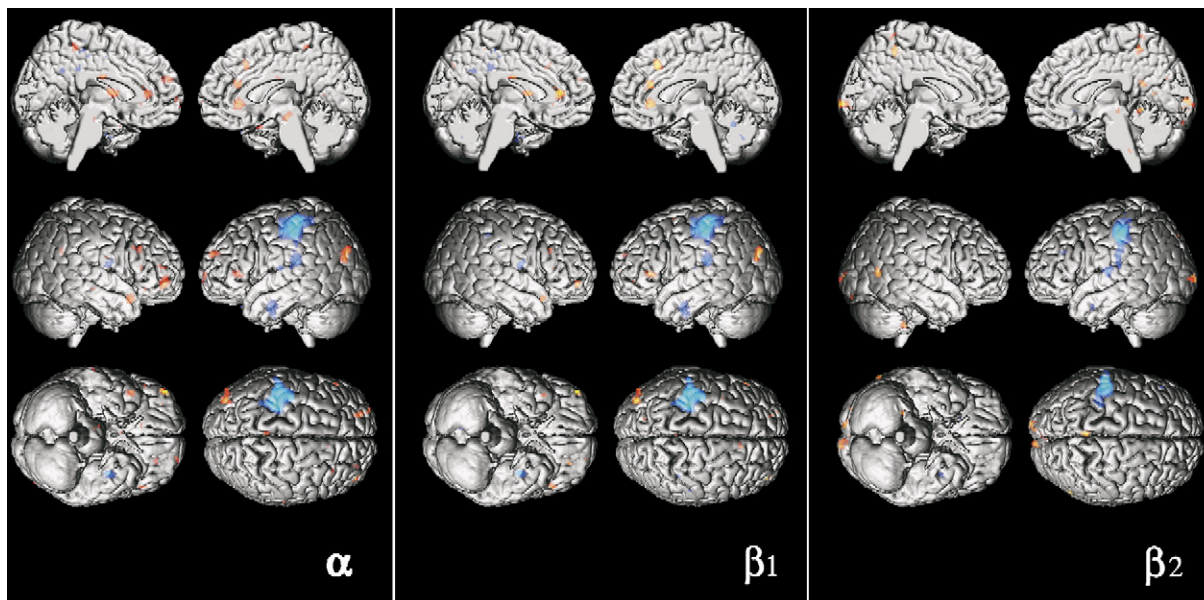


Fig. 4. Statistical parametric maps of positive (yellow-red) and negative (aqua-blue) correlation between rCBF and left sensorimotor EEG alpha, beta1 and beta2 power during each task, superimposed on surface-rendered MRI. Areas that survived a statistical threshold of $p < 0.001$ uncorrected for multiple comparisons are shown. A significant negative correlation between the left sensorimotor alpha and beta1 power and rCBF was found in the left pre- and postcentral gyrus. A significant negative correlation between the left sensorimotor beta2 power and rCBF was found in the left postcentral gyrus.

A significant positive correlation between the right sensorimotor beta1 power and rCBF was found in the left lateral prefrontal cortex and the left superior occipital gyrus (Fig. 5B, Table 3B). No significant positive correlation was found between the right sensorimotor beta2 power and rCBF was found (Fig. 5C, Table 3B).

Discussion

This is the first report of quantitative evaluation of the correlation between rCBF changes and regional EEG powers. Significant negative correlations between the occipital EEG power within the

alpha and lower beta bands and the occipital rCBF were observed. There were also significant negative correlations between the left and right sensorimotor EEG power within the alpha and beta ranges and the ipsilateral sensorimotor rCBF, respectively. These findings suggest that decrease in the regional EEG rhythm at around 10–20 Hz might represent the neuronal activation of the cortex underlying the electrodes, at least for the visual and sensorimotor areas. Since the animal experiments suggested that low amplitude desynchronized EEG is associated with the increased excitability in thalamocortical system (Steriade and Llinas, 1988), it is possible that the decrease of human scalp-recorded EEG power reflects cortical activation (Pfurtscheller, 1992).

Table 2

Brain regions (A) negatively and (B) positively correlated with the left sensorimotor EEG power

EEG band	Region	BA	Coordinate Talairach space			Cluster-level corrected P	kE	z
			x	y	z			
<i>(A) Negative correlation</i>								
Alpha	Lt precentral gyrus (GPrC)	4	−32	−25	51	0.000	1550	5.19
	Lt postcentral gyrus (GPoC)	3	−38	−19	47			
	Lt inferior parietal lobule (LPi)	40	−40	−31	35			
Beta1	Lt precentral gyrus (GPrC)	4	−30	−25	49	0.000	1396	4.96
	Lt postcentral gyrus (GPoC)	3	−38	−19	47			
Beta2	Lt postcentral gyrus (GPoC)	2	−51	−21	45	0.000	964	4.58
	Lt inferior parietal lobule (LPi)	40	−42	−27	42			
	Lt postcentral gyrus (GPoC)	40	−61	−22	18			
<i>(B) Positive correlation</i>								
Alpha	No suprathreshold clusters							
Beta1	No suprathreshold clusters							
Beta2	No suprathreshold clusters							

Clusters that survived a statistical threshold of $p < 0.05$ corrected for multiple comparisons are shown.

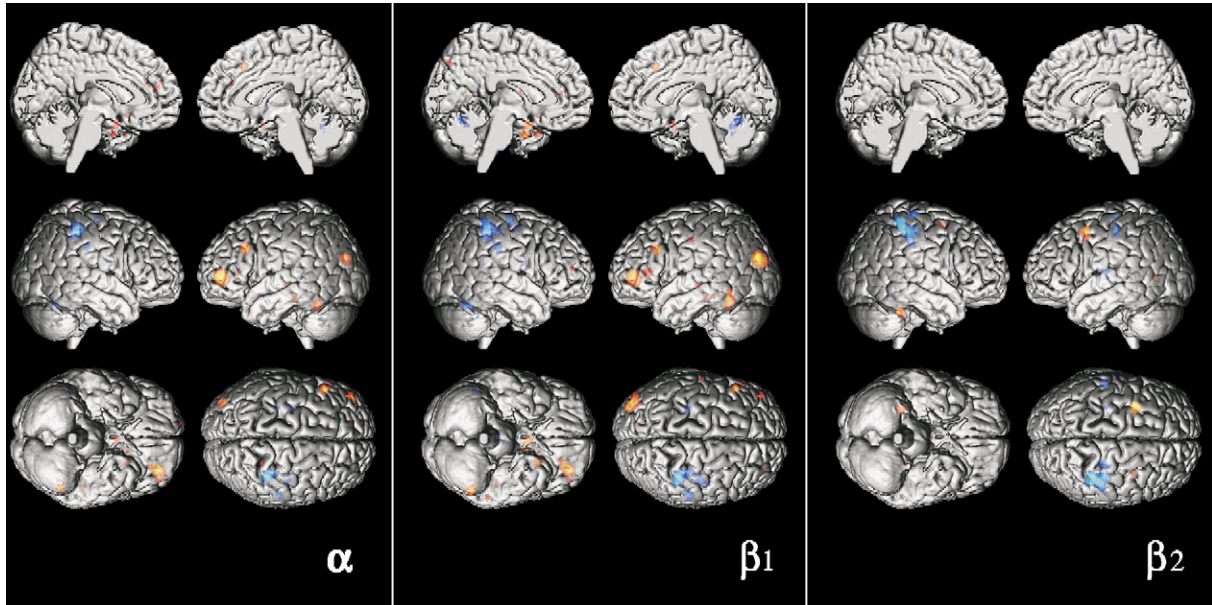


Fig. 5. Statistical parametric maps of positive (yellow-red) and negative (aqua-blue) correlation between rCBF and right sensorimotor EEG alpha, beta1 and beta2 power during each task, superimposed on surface-rendered MRI. Areas that survived a statistical threshold of $p < 0.001$ uncorrected for multiple comparisons are shown. A significant negative correlation between the right sensorimotor alpha, beta1 and beta2 power and rCBF was found in the right postcentral gyrus. A significant positive correlation between the right sensorimotor alpha and beta1 power and rCBF was found in the left middle frontal gyrus.

The occipital EEG power showed a positive correlation especially with the rCBF of the prefrontal cortex and the right sensorimotor EEG power showed a positive correlation with the rCBF of the left prefrontal cortex. These results suggest that the neural network including the prefrontal cortex especially on the left could play an important role to generate the EEG rhythm in both occipital and sensorimotor cortices.

Negative correlations of rCBF with the sensorimotor mu rhythm

By investigating the linear relationship between the sensorimotor alpha power and rCBF, we showed that the left and right mu

rhythms have a significant negative correlation with the ipsilateral sensorimotor cortical activation. Because differences in source localization, frequency, power, and functional responsiveness suggest independent sources for mu and occipital alpha rhythms (Pineda, 2005), we performed the rCBF correlation analysis using SPM by setting the occipital alpha power as a statistical nuisance value to evaluate the purely sensorimotor mu rhythm, although the general linear model might not properly eliminate the “nuisance” effect. In addition, we evaluated multiple motor tasks in the present study to minimize a task-specific effect on rCBF change.

Although overlapping each other in the frequency range, the sensorimotor mu and occipital alpha band rhythms rather reflect

Table 3
Brain regions (A) negatively and (B) positively correlated with the right sensorimotor EEG power

EEG band	Region	BA	Coordinate Talairach space			Cluster-level corrected P	kE	z
			x	y	z			
<i>(A) Negative correlation</i>								
Alpha	Rt inferior parietal lobule (LPi)	40	40	-33	44	0.034	266	4.23
	Rt postcentral gyrus (GPoC)	3	36	-23	47			
Beta1	Rt inferior parietal lobule (LPi)	40	42	-35	44	0.001	529	4.44
	Rt postcentral gyrus (GPoC)	3	36	-23	47			
Beta2	Rt inferior parietal lobule (LPi)	40	46	-34	57	0.001	570	4.33
	Rt postcentral gyrus (GPoC)	40	44	-27	47			
	Rt postcentral gyrus (GPoC)	3	53	-23	38			
<i>(B) Positive correlation</i>								
Alpha	Lt middle frontal gyrus (GFm)	10	-32	49	-1	0.037	261	4.48
Beta1	Lt middle frontal gyrus (GFm)	10	-30	47	-2	0.048	242	4.28
	Lt inferior frontal gyrus (GFi)	10	-36	45	5			
	Lt middle frontal gyrus (GFm)	11	-24	40	-9			
	Lt superior occipital gyrus (GOs)	19	-32	-76	24			
Beta2	No suprathreshold clusters							

Clusters that survived a statistical threshold of $p < 0.05$ corrected for multiple comparisons are shown.

two distinct physiological phenomena, which was also supported by the present results (Vanni et al., 1999). It has been reported that self-paced hand movement can induce a contralateral localized mu rhythm ERD and an occipital localized alpha band rhythm ERS at the same time (Pfurtscheller and Lopes da Silva, 1999). In direct recordings from cat visual and somatosensory cortices while both alpha and mu rhythms occurred under similar behavioral conditions, their bursts were independent and had low coherence (Rougeul-Buser and Buser, 1997).

In human scalp EEG, the main peak frequency of the mu rhythm is within the alpha band, which mainly covers a frequency range between 7 and 14 Hz with a mean frequency around 10 Hz or even slightly below (Pfurtscheller et al., 2000). However, its distribution is over the bilateral hand SM1, and its power is particularly sensitive to the motor tasks. The blocking of mu rhythm caused by movements of the body part is specific to somatic representation areas of the cortex (Arroyo et al., 1993). The time course of the mu rhythm amplitude shows a specific biphasic pattern, which is known as ERS/ERD (Pfurtscheller, 1977; Pfurtscheller and Lopes da Silva, 1999). Consequently, the 10-Hz mu rhythm increase might reflect a resting state or even inhibition in the sensorimotor system (Pfurtscheller, 1992; Salmelin and Hari, 1994). Our findings are in accord with the 'idling' rhythm hypothesis of the mu rhythm (Kuhlman, 1978). Moreover, the power suppression of the mu rhythm produced by a motor task (Crone et al., 1998; Gerloff et al., 1998; Pfurtscheller and Berghold, 1989; Toma et al., 2002; Toro et al., 1994) may reflect cortical activation at SM1 in a parametric way.

Although the limited spatial resolution of the rCBF measurement using PET cannot allow us to precisely differentiate S1 and M1, the parietal cortex including the postcentral gyrus and inferior parietal lobule showed a greater negative correlation than the frontal cortex including the precentral gyrus in this study. The previous PET study using a simple repetitive finger movement task also showed activation of both S1 and M1 (Mima et al., 1999). The activation of S1 may be due to the somatosensory afferent feedback from the periphery or the motor efferent copy conveyed from M1. It is also possible that the activity of S1 is related to preparation for motor action because some studies showed attenuation of the postcentral mu rhythm prior to voluntary movements (Nagamine et al., 1996; Ohara et al., 2000; Salmelin et al., 1995). Based on the recent results showing a specific motor deficit in movement initiation after an inferior parietal lobule lesion (Mattingley et al., 1998), the inferior parietal lobule has been suggested as a candidate area for higher-order motor function. Since coherent cell assemblies over at least several square centimeters are necessary (Cooper et al., 1965; Lopes da Silva, 1991) for the generation of the scalp-recorded EEG rhythmicity, both M1 and the parietal cortex are likely to be associated with the 'idling' of the mu rhythm.

Negative correlations of rCBF with the sensorimotor beta band rhythm

In this study, the activated areas that were negatively correlated with the sensorimotor alpha, beta1 and beta2 power showed similar cortical distributions. It has been well accepted that the beta band rhythm at SM1 might play an important role in motor control. Cortico-muscular coherence studies suggested that the central beta band rhythm may convey the motor command from M1 to the motor units (Conway et al., 1995; Mima et al., 2000; Salenius et

al., 1996). It has also been reported that the somatosensory beta band rhythms around 18 Hz in monkeys distribute over the SI hand area and the posterior parietal cortex and are blocked by the smallest body movement (Rougeul et al., 1979). Beta desynchronization during voluntary hand movement occurred in parallel with the mu ERD in the alpha band (Pfurtscheller, 1981).

Electrocorticogram and magnetoencephalography studies suggested that the 10 Hz rhythm could appear to arise from the somatosensory cortex, whereas the 20 Hz rhythm could arise predominantly from the precentral gyrus (Hari and Salmelin, 1997; Pfurtscheller, 1992; Salmelin et al., 1995; Salmelin and Hari, 1994). However, this topographic distribution is still controversial because electrocorticogram studies showed no consistent difference in distribution between the 10 Hz rhythm and the 20 Hz rhythm (Crone et al., 1998; Ohara et al., 2000). The rCBF changes in our study did not reveal this anterior–posterior tendency. However, this might be due to the limited spatial resolution of the PET methodology.

Negative correlations of rCBF with the occipital rhythm

The thalamocortical and corticocortical systems are supposed to interact in the generation of cortical alpha band rhythms (Steriade et al., 1990). In this study, the occipital alpha EEG had a significant negative correlation with the bilateral occipital rCBF, which extended broadly from the primary to association cortex. The result is in accordance with the previous reports (Leuchter et al., 1999; Sadato et al., 1998). Extensive involvement of the primary and association visual cortex is consistent with the finding that the alpha band rhythm can be suppressed not only by opening of the eyes but also by visual imagery, which suggests that the suppression of alpha band rhythm can be associated with higher visual processing (Hari and Salmelin, 1997).

Although previous studies revealed that the rCBF change (Larson et al., 1998; Sadato et al., 1998) or the glucose metabolic change (Schreckenberger et al., 2004) in the thalamus correlates with the global alpha power, our result showed no significant correlation between the regional occipital alpha EEG and the activation of thalamus. Therefore, it is possible that the generator mechanism of the whole brain alpha band rhythm and regional (occipital) alpha band rhythm might be different and that the thalamus is related to the production of the former but not so much for the latter. Electrophysiological evidence from isolated cerebral cortex determined that cortical circuits were capable of generating alpha band rhythms quite independently of thalamic influences (Kristiansen and Courtois, 1949). In addition, it has been reported that the corticocortical alpha coherence values were higher than any thalamocortical coherence (da Silva et al., 1973; Lopes da Silva et al., 1980) and relatively independent of thalamic influences (Lopes da Silva et al., 1980).

In this study, a similar correlation with rCBF was observed for the occipital alpha and beta1 power. When a subject concentrates on a particular modality, the EEG activity in the alpha and/or lower beta band specifically decreases in the corresponding brain region (Neuper and Pfurtscheller, 2001). Therefore, our result suggests that the same neurophysiological mechanism as the occipital alpha band rhythm could be associated with the occipital beta1 band rhythm generation. However, the similar correlation might be caused by a harmonic of the alpha activity because alpha activity is often not sinusoidal and it is very difficult to differentiate such a harmonic from beta band rhythms.

Positive correlations of rCBF with the sensorimotor and occipital rhythm

A significant positive correlation was found between the right sensorimotor alpha power and the rCBF of the left middle prefrontal gyrus, which extended to the dorsolateral prefrontal cortex (BA 9/46) (Ramnani and Owen, 2004). The sensorimotor mu rhythm is associated with motor behavior (Pfurtscheller et al., 1996). Although no direct connections have been reported between the dorsolateral prefrontal cortex and SM1, the dorsolateral prefrontal cortex sends the strongest projections to the premotor system in the macaque monkey brain (Lu et al., 1994). The premotor area could influence motor control (Tokuno and Nambu, 2000) via its dense corticocortical projections to M1 (Dum and Strick, 2002; Shimazu et al., 2004). Our result suggests that the corticocortical network between the prefrontal cortex and the SM1 via the premotor cortex might be associated with the generation of the sensorimotor mu rhythm, especially on the right. On the other hand, the left sensorimotor EEG power did not show any significant positive correlations. The EEG study using an independent component analysis suggested independent mu sources in the two hemispheres (Makeig et al., 2002). Therefore, the asymmetric results in our study might explain the independent generation of the sensorimotor mu rhythm in the two hemispheres. However, further researches would be necessary to elucidate the exact role of left middle frontal gyrus for the generation of mu rhythm.

A significant positive correlation between the right sensorimotor beta1 power and rCBF was found in the left lateral prefrontal cortex which is similar to the right sensorimotor mu power. Our result suggests that the corticocortical network including the prefrontal cortex and SM1 could be associated with the generation of the sensorimotor beta1 band rhythm as well as the mu rhythm in the alpha band. In a previous study (Nakamura et al., 1999), the rCBF in the left lateral prefrontal cortex was demonstrated to be positively correlated with the global beta power. Beta activity has recently been ascribed to the general role of an ‘attention-carrier’ (Wrobel, 2000) and associated with behavioral arousal and attentional processes (Nofzinger et al., 2000). States of attention and motor preparation were suggested to be particularly associated with increased levels of beta activity in the cat (Bouyer et al., 1981) and the monkey motor cortex (Rougeul et al., 1979) in local field potential studies. These reports suggest that focused attention for the motor preparation might be associated with the sensorimotor beta1 band rhythm and the prefrontal cortex (Steriade, 1993).

A significant positive correlation between the occipital alpha power and rCBF was found in both lateral and medial prefrontal cortices and basal forebrain mainly on the left, which is consistent with the previous study (Sadato et al., 1998) that showed a positive correlation between the alpha power and the rCBF in the limbic system including basal prefrontal cortex. A similar positive correlation was also found between the occipital beta1 power and rCBF. The orbitofrontal cortices are associated with social–affective and motivational aspects of frontal lobe function (Rolls, 2004). Anatomically, the orbitofrontal cortices have widespread connections with a distributed ascending activating system including the pontine reticular formation, basal forebrain, amygdala, hippocampus, temporal pole, insula, cingulate cortex and parahippocampal gyrus (Morecraft et al., 1992), placing them in a position to integrate limbic–paralimbic afferents with those coming from higher order association cortex and subsequently influence motivational, emotional and arousal systems in the brain (Nofzinger et al., 2000). The

positive correlation between the occipital alpha and beta1 power and neuronal activities in the limbic system including anterior cingulate cortex and orbitofrontal cortex may provide a neuroanatomical basis for studies of the relationship between emotional state and occipital alpha and beta1 band rhythm. The global alpha band rhythms have also been explored as a possible indicator of emotional states (Drennen and O’Reilly, 1986) and increased attention has been focused on the association of local alpha oscillations, including the occipital alpha oscillations, with cognitive operations (Klimesch, 1996, 1997). An interaction between anterior and posterior cortical circuits in the generation of human alpha rhythms has been supported by EEG coherence studies (Cantero et al., 1999, 2000; Srinivasan, 1999; Thatcher et al., 1986). This functional relationship could be anatomically supported by the superior longitudinal fasciculus traveling parallel to the midline (Cantero et al., 2002).

These findings suggest that the neural network for generating the EEG rhythm in both occipital and sensorimotor cortices might be similar and nonspecific. Studies using the frontal midline (mental) theta activities suggest that the prefrontal cortex including the anterior cingulate cortex might work as a generator of the state of internalized attention, which means manipulation of one’s attentional focus during meditation (Aftanas and Golosheikine, 2001; Ishii et al., 1999; Sasaki et al., 1996). Thus, it is likely that the apparent positive correlation between the prefrontal activation and the increased idling rhythm at the sensorimotor or visual cortex can be due to the state of internalized attention facilitated by the rest condition with eyes closed.

EEG and PET methodology

Although the H₂¹⁵O tracer has much shorter time frame than the 18-fluoro-deoxyglucose tracer (20–30 min) and the results of H₂¹⁵O PET examinations directly depend on the acute cerebral state of activation during tracer injection (Schreckenberger et al., 2004), it is also true that the simultaneous PET and EEG recordings reflect EEG signals and cerebral blood flow changes which were temporally averaged over the span of 60 s. This diminished time resolution may be one of the limitations of the inter-modality correlation. However, it is likely that the EEG power should be stable during the PET scan time in the present study because we applied the simple repetitive movement tasks, in which the estimation of the task-related power change of the EEG was found to be useful (Andres et al., 1999; Gerloff et al., 1998; Toma et al., 2002).

Various types of EEG reference techniques may have different advantages and disadvantages for the EEG power estimation (Nunez et al., 1997). In the present study, we used the digitally linked earlobe reference. It is possible that the earlobe reference signal may contain the task-related EEG activity. However, none of our EEG electrodes (C3, C4, FC3, FC4, O1, O2) was located closer than ~6 cm to the reference electrodes, which may minimize the contribution of reference activation. To minimize the effect of common reference signal that is inevitably contaminated in the referenced EEG recording, we used the covariance analysis in which the task-related change of the EEG power and the task-related change of rCBF were compared.

Acknowledgments

This study is partly supported by the Grants-in-Aid for Scientific Research on Priority Areas (Integrative Brain Research) for T.M. (18019020) and (System study on higher-order brain functions) for

H.F. (18020014) from the MEXT of Japan, Grant-in-Aid for Scientific Research (C) 18500239 for T.M. from Japan Society for the Promotion of Science.

We would like to thank Dr. Hiroshi Shibasaki for useful comments.

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