
Propagation of EEG activity during finger movement and its imagination

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Abstract. We investigated the pattern of EEG activity propagation in the beta and gamma band during a finger movement experiment and imagination of that task. The data were analyzed by means of a short-time directed transfer function (SDTF) based on a multivariate autoregressive model. The signals from the right (or left) hemisphere were processed simultaneously (not pairwise), which is crucial for obtaining a correct picture of EEG activity transmissions. The pattern of propagation in the beta band involved for both tasks a decrease of the propagation from the motor areas during the execution of the movement – less pronounced in the case of imagination. The performance of the motion was mainly connected with a short outburst of gamma activity from the hand sensorimotor areas. In case of imagination the gamma outflow lasted longer and concerned larger brain areas.

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Key words: EEG activity propagation, motor task, motor control, movement imagery, multivariate autoregressive model (MVAR), short-time directed transfer function (SDTF), beta activity, gamma activity propagation

INTRODUCTION

During the last years the investigation of EEG activity accompanying voluntary movement has been in the center of attention (review by Pfurtscheller and Lopes da Silva 1999, Pfurtscheller et al. 2003), however most studies concern the amplitude of the EEG rhythms in connection with their topography. Much less attention has been paid to the phases, which contain information about the relation between signals and their propagation within the brain (Ginter et al. 2001). There exists rich evidence that synchronized oscillatory activity of neural assemblies subserves information processing by linking neuronal groups with similar functional state and that oscillatory activity of local field potentials plays a role in spatially selective multiregional cortical binding (Lopes da Silva 1992). Hence, study of the role of EEG rhythms and their propagation can bring valuable evidence concerning the mechanisms of the information processing in the brain.

Starting from the early eighties there were several attempts to find an estimator describing signal propagation (Inouye et al. 1995, Saito and Harashima 1981), however, the proposed estimators were only able to calculate directionality between two channels at a time. This was also the case for more recent measures of directionality (Bernasconi and Konig 1999, Freiwald et al. 1999). It has been shown (Blinowska et al. 2004, Kuś et al. 2004) that bivariate methods for the assessment of directionality, no matter if they are based on phases of bivariate coherences or bivariate Granger causality measure (Granger 1969), are likely to give misleading results. Comparison of different methods for the assessment of directionality may be found in Kuś and coauthors (2004).

The multivariate estimator of propagation, called the Directed Transfer Function (DTF), is designed for an arbitrary number of channels, and was introduced already in 1991 (Kamiński and Blinowska 1991). This DTF function was applied successfully to localize epileptic foci (Franaszczuk and Bergey 1998), to determine LFP propagation between brain structures of animals in different behavioral states (Korzeniewska et al. 1997), and to investigate EEG propagation in different sleep stages (Kamiński et al. 1997). Investigation of the dynamics of brain activ-

ity propagation that is important for understanding information processing requires estimators dependent on time. Such a measure is provided by the Short-time Direct Transfer Function (SDTF) – a modification of DTF dependent not only on frequency but also on time (Kamiński et al. 2001). SDTF is based on the ensemble averaging paradigm, which allows the calculation of the estimator for short data windows when multiple realizations of a process are available.

The SDTF has already been applied to the evaluation of motor task experiments. A study performed on 3 subjects involved the comparison of the results with a high resolution time-frequency method of signal analysis – matching pursuit. A consistent pattern of propagations was found for alpha and beta rhythms, which confirmed the validity of the method (Ginter et al. 2001). In another experiment involving imagination of movement, the SDTF method revealed the importance of the gamma rhythm and the connection between the beta and gamma rhythms (Ginter et al. 2005). In this paper we shall pursue the problem of determining the pattern of EEG flows in case of a real finger movement and its imagination, by application of SDTF for a larger group of subjects performing both tasks. The aim of the paper is finding of the similarities and differences in the pattern of propagation of the brain rhythms during a real motor task and its imagination.

In this paper we shall concentrate on the beta and gamma rhythms. It has been shown that they have different synchronization properties (Kopell et al. 2000) and that in motor control tasks a decrease of beta may be accompanied by an increase in the gamma band (Ginter et al. 2005). Beta rhythm is connected with the processes of attention (Wróbel 2000) and expectation (Buser and Rougeul-Buser 1995). Gamma activity has been interpreted as the information carrier (Bressler 1990) essential for binding processes and feature linking (Singer and Gray 1995). In experiments involving subdural electrodes the role of gamma activity in motor control was found to be essential (Crone et al. 1998, Pfurtscheller et al. 2003). The role of theta activity was demonstrated in different kind of experiments, involving slow periodic movements, where the intermittent motor control was connected with synchronized 6–9 Hz activity in cerebello-thalamo-cortical loop (Gross et al 2002).

METHODS

Material and data acquisition

The experiment was performed on 9 right handed volunteers: 8 males and one female, 21–27 years old. An EEG was acquired using the Braintronics ISO-1064 CE apparatus (Elmico, Poland), from 30 electrodes located in the positions as used in the extended 10-20 system (Fig.1a). The signal was filtered in the 0.5–100 Hz band and sampled with a frequency of 250 Hz. The 50 Hz artifact produced by mains was eliminated by a digital filter. The surface EMG was recorded from both hands in order to find and eliminate the data epochs for which the tension of the hand muscles occurred during imagination task.

During the experiment the subject was lying in a dimly lit room observing a computer monitor. Every 10–14 s a short sound was delivered, 3–5 s after which a fixation cross appeared on the monitor for 2 s. Then an arrow (cue) was presented for a period of 1.25 s, indicating randomly a left or right direction. The subject was instructed to lift up his/her left or right hand index finger (depending on the direction of the arrow) for 1 s or to imagine this movement. The schema of one repetition is presented in Fig.1b. Each session consisted of 130 repetitions. The experimental setting was designed in the same way for both tasks in order to make real and imaginary actions comparable. The experiment consisted

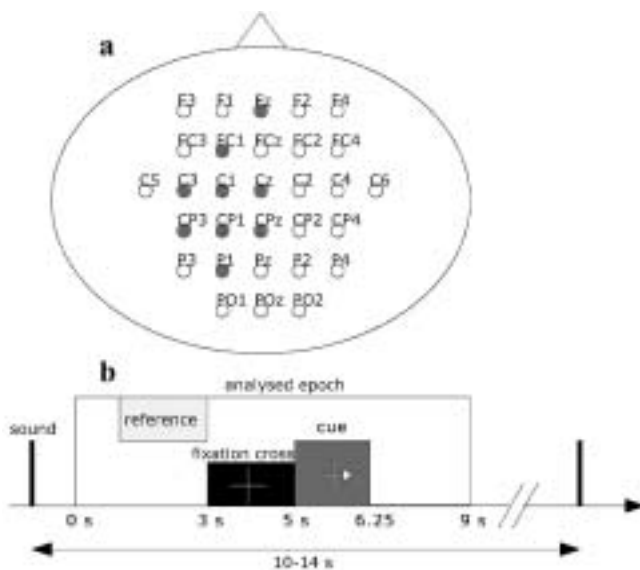


Fig. 1. Placement of the electrodes (a) and scheme of the experiment (b)

of four alternating sessions, two for real and two for imaginary movements (beginning with real movements).

The signal was sub-sampled to a sampling frequency of 125 Hz and divided into 9 s long epochs with cue onset in the fifth second. Epochs containing muscle artifacts were rejected. In order to better recognize artifacts generated by contraction of neck muscles, the EEG signals were visually scored, for each subject a certain threshold was established for energy cumulated in the 15–40 Hz band during an epoch, and trials surpassing this threshold were rejected. We took these special measures to eliminate high frequency artifacts because in this experiment we concentrate on changes of flows in the beta and gamma bands.

Multichannel data analysis

The MVAR model and DTF have been described in earlier publications, e.g. Kamiński and Blinowska (1991), Blinowska and coauthors (2004), and Kamiński and Liang (2005). The SDTF method has been described among others in Ginter and colleagues (2001) and Kuś and others (2004), therefore we will only briefly sketch it below.

The DTF method is based on fitting a multivariate autoregressive (MVAR) model to the signals (Franaszczuk et al. 1985). In terms of the model a k -channel process can be represented as a vector \mathbf{X} of k EEG signals recorded in time: $\mathbf{X}(t) = (X_1(t), X_2(t), \dots, X_k(t))$. Then the MVAR model can be expressed as:

$$\mathbf{X}(t) = \sum_{i=1}^p \mathbf{A}(i)\mathbf{X}(t-i) + \mathbf{E}(t), \quad (1)$$

where $\mathbf{X}(t)$ is the data vector at time t , $\mathbf{E}(t)$ is the vector of white noise values, $\mathbf{A}(i)$ are the model coefficients and p is the model order. This equation can be rewritten in the form:

$$-\sum_{i=0}^p \mathbf{A}(i)\mathbf{X}(t-i) = \mathbf{E}(t), \quad \mathbf{A}(0) = -\mathbf{I} \quad (2)$$

where \mathbf{I} – identity matrix. The coefficients of the model were estimated from the correlation matrix of the signals by means of Yule–Walker algorithm (Marple 1987). The model order can be determined by means of criteria derived from information theory; the AIC criterion (Akaike 1974) was found to be the most

satisfactory and here it was used for MVAR model fitting; usually a model order of 5 was used.

After transforming the model equation to the frequency domain we get:

$$\mathbf{X}(f) = \mathbf{A}^{-1}(f)\mathbf{E}(f) = \mathbf{H}(f)\mathbf{E}(f). \quad (3)$$

The $\mathbf{H}(f)$ matrix is called the transfer matrix of the system, f denotes the frequency. We can consider MVAR as a black box model with a vector of noise as input, EEG signals as output and the spectral characteristics and relations between signals contained in the transfer matrix $\mathbf{H}(f)$. Matrix $\mathbf{H}(f)$ is not symmetric and its non-diagonal elements give information about the causality relations between the corresponding channels.

The non-normalized DTF describing the transmission from channel j to i is defined as $|H_{ij}(f)|$, i.e. the corresponding non-diagonal ($i-j$) element of the transfer matrix of the model:

$$DTF_{ij}(f) = |H_{ij}(f)| \quad (4)$$

We have used here the Directed Transfer Function in its non-normalized form, which is equivalent to the Granger causality (Granger 1969) extended to an arbitrary number of channels (Kamiński et al. 2001). DTF is robust in respect of noise, it identifies correctly the propagation in the presence of noise that is several times higher than the signal itself and is insensitive to constant phase disturbances (Kamiński and Liang 2005, Kamiński et al. 2001). Volume conduction involves propagation of the electromagnetic field with the light velocity, hence there are no delays between channels – it is zero phase propagation. DTF effectively discriminates against volume conduction, since it detects the differences of phases.

The causality relations between channels mean that the variance in a given channel may be explained using the past samples of the other channels of the set. The direction of the signal transmission coded in cross-correlations between signals and contained in the cross-correlation matrix of the MVAR model is translated into phase shifts by transformation to the frequency domain. This phase dependencies are expressed in the transfer matrix $\mathbf{H}(f)$. The value of $DTF_{ij}(f)$ shows whether the signal component of a given frequency f in channel j is shifted in time with respect to the signal

component of the given frequency in channel i . The estimate shows only the direction, not the value of the delay. However, the information is unambiguous, contrary to the Fourier estimate, which gives the phase modulo 2π . In this paper the terms “EEG activity propagation” or “EEG activity flow” mean that an EEG wave appears earlier at a given location than at another location, which follows from the phase differences.

The coefficients of the MVAR model are estimated from the correlation matrix. When multiple repetitions of the experiment are available, the correlation matrix can be found by ensemble averaging over realizations:

$$\tilde{R}_{ij}(s) = \frac{1}{N_T} \sum_{r=1}^{N_T} R_{ij}^{(r)}(s) = \frac{1}{N_T} \sum_{r=1}^{N_T} \frac{1}{n-|s|} \sum_{t=1}^{n-|s|} X_i^{(r)}(t) X_j^{(r)}(t-s) \quad (5)$$

where N_T is the number of realizations, $R_{ij}^{(r)}(s)$ denotes the elements of $\mathbf{R}^{(r)}(s)$ – the correlation matrix calculated for time lag $t=s$ in realization r , and n is the length of the data window.

In this approach the model is fitted to the short data windows, then correlation matrix (Eq.5) is found by ensemble averaging and consecutively model coefficients and DTFs are computed for a given short epoch. Then the data window is shifted with overlap and in this way, by means of a short sliding window, time-varying DTF, called SDTF (Short-time Directed Transfer Function), can be found.

MVAR is a parametric model and obviously the number of parameters must be much lower than the number of data points. The number of parameters is pk^2 , where p is the model order and k is a number of channels, whereas the number of data points is given by knN , where n is the window length and N is the number of repetitions. This requirement limits the length of the data window (which cannot be too short because of statistical requirements) and effectively influences also the time resolution. A compromise must be found between the window length and the number of channels. It is recommended to use as many channels as possible in order to take into account all possible interactions. The signals from all crucial locations should be simultaneously processed. Here we have evaluated simultaneously 9 channels and we have chosen a window size of 50 points, (400 ms) length, which resulted in a ratio of data points to number of parameters of about 50. In order to calculate SDTF as a function of time the window position was consecutively shifted by 10 points (80 ms).

Two separate sets of 9 electrodes were taken into account, one located over the left hemisphere sensorimotor area and another at the opposite positions over the right hemisphere; the middle electrodes were shared by both sets (see Fig. 1a). Signals from distinct hemispheres could be treated separately because of little coherence and weak flow found between them. Before the actual calculations we had estimated partial coherences and DTFs for signal set involving both hemispheres and they were below the significance level. These preliminary calculations of interhemispheric coherences are consistent with investigations of Andrew and Pfurtscheller (1999).

Statistical estimation of flow changes

In order to find statistical significance of flow changes related to the subject's action, a method based on a bootstrap technique was applied (Efron 1979). In this approach, the variance of the function is obtained by repeated calculation of the results for a randomly selected pool of original trials. Selecting a random pool of trials corresponds to simulating another experimental session. Signals recorded in the period 5 to 3 seconds before cue onset were considered as reference and a null hypothesis of a lack of changes was tested in respect of probability distribution in this epoch. From N different signal realizations, a set of N not necessarily different realizations was drawn and the MVAR model coefficients and, subsequently, the SDTFs for reference time were computed. This selection procedure was repeated 100 times (1000 times drawing provided practically no change in the significance level). By gathering the values of SDTF obtained in all time-windows of the reference epoch after all drawings, a distribution of reference values was constructed. On the basis of this distribution the confidence interval may be found. Our null hypothesis was no decrease (or no increase) of outflow at a given time epoch in relation to the reference. The hypothesis was rejected with a 2% confidence level if the SDTF value was below the 2-percentile (or above the 98-percentile).

RESULTS

Characteristics of beta activity flows

Since we concentrated mainly on beta and gamma activity, in order to better observe the changes of flows

in these frequency bands, we have filtered out alpha activity. In Fig. 2a the SDTFs are shown as functions of time and frequency. When analyzing the matrix of SDTFs reflecting the propagation between the channels, one can see bigger dynamics of outflows from the areas of primary motor cortex which are responsible for hand movement (color coded DTFs fluctuate in time, especially a gap in propagation is visible after presentation of a cue – around second 5–6) in comparison to outflows from other areas, where the pattern is more stable. In order to better follow the time course of propagation for beta and gamma rhythms, the SDTF values were integrated in the 17–23 Hz and 35–41 Hz bands (Fig. 2b). In the time course of outflows in the beta band three characteristic phenomena dominate: the increase of activity immediately after cue onset (second 5), its decrease during task performance and a subsequent rebound. These phenomena are illustrated in Fig. 2b, where the time evolution of propagations in beta and gamma bands are shown. The increases or decreases of the flows above significance levels are marked by the circles.

In Fig. 3 a summary of the results for all subjects in case of movement of the right hand finger for a pre-movement epoch (0–0.5 s) after cue onset is shown. For that period the strongest outflow was observed from electrode C1 for most subjects (Fig. 3). Before imagination of the right hand finger movement this increase was also present, mainly in the left part of the head, although only for some subjects it was well localized both topographically and in time. For the left hand finger movement or its imagination, the increase rarely appeared.

In the epoch 0.3–1.5 s after cue onset for the left hand finger movement a decrease of outflow of beta activity was localized on the right side of the head in the neighborhood of electrode C2. For the right hand finger movement the decrease was visible in both hemispheres, however, it was most pronounced for electrode Cp3. The flow of beta activity between channels overlying sensorimotor areas decreased also during the movement imagination. Nevertheless, in this case the duration of the decrease was shorter than for real movement and many times it was not strong enough to be statistically significant. The decrease in propagation in the beta band during finger movement was also observed in Ginter and coauthors (2001) and in case of imagination in Ginter and others (2005).

After the task (1–3 seconds after the presentation of

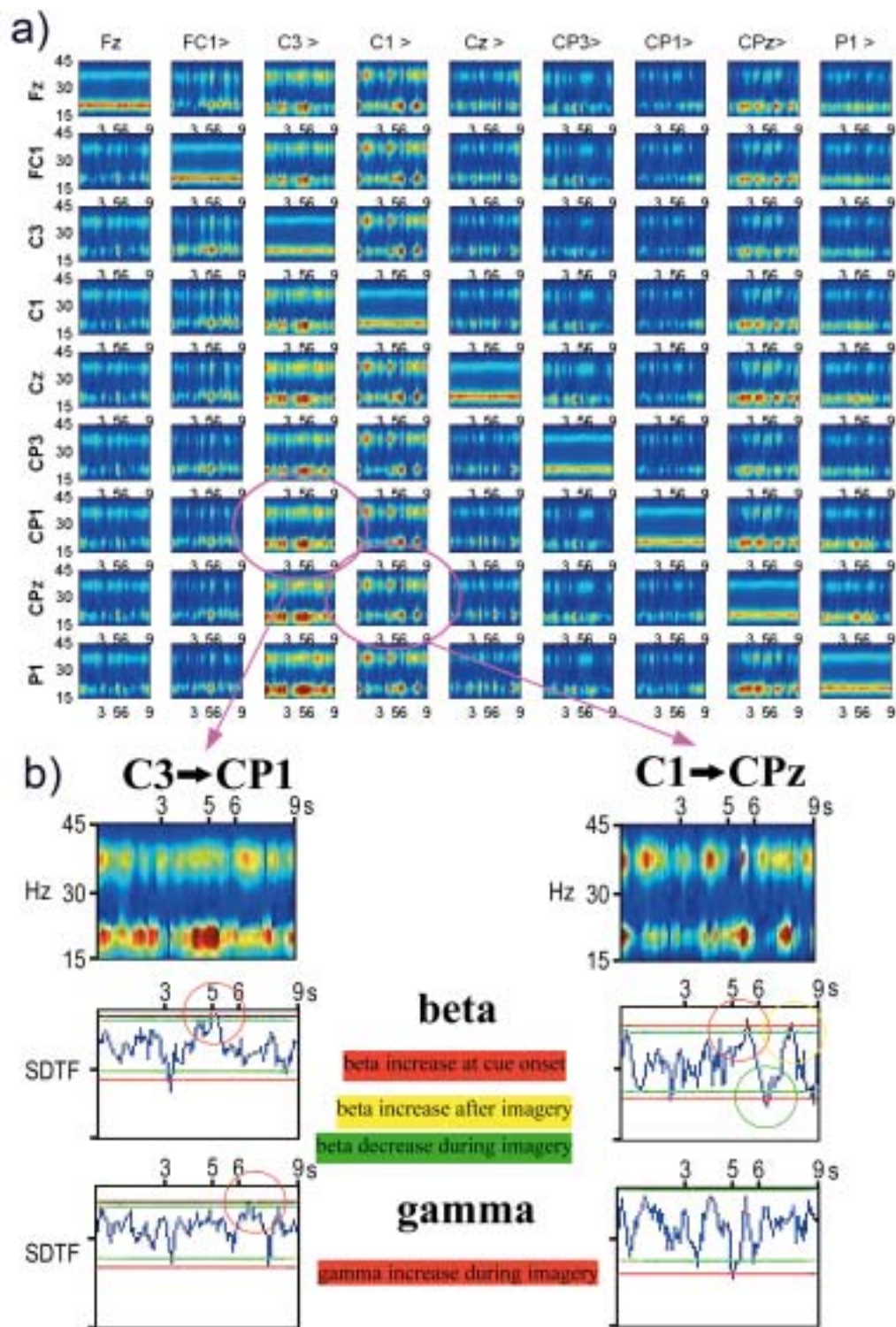


Fig. 2. (a) Propagation of EEG activity in the left hemisphere during right hand movement imagination for one subject. In each small panel SDF is presented as a function of time (horizontal axis in seconds) and frequency (vertical axis in Hz). The intensity scale coded by colors (red the strongest) is the same for all panels. The flow of activity goes from the electrode marked above the column to the electrode marked at the left. (b) The upper pictures are enlarged panels from the matrix presented in (a). The lower pictures represent the corresponding beta and gamma flows represented by SDF functions integrated in the frequency bands (17–23 Hz) and (35–41 Hz).

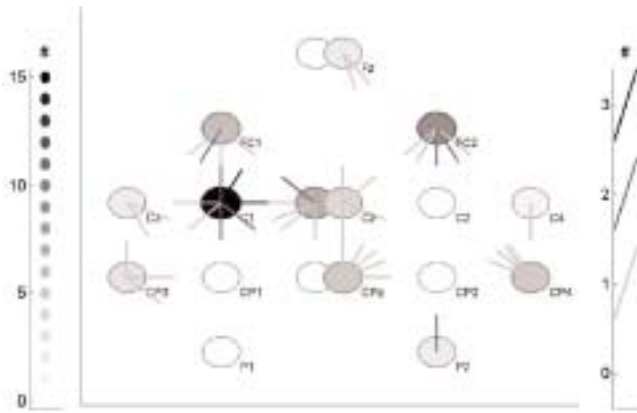


Fig. 3. Increase of beta propagation before movement (0–0.5 s after the cue presentation) of the right hand. The directions of flows are presented by lines, their shades depend on the number of cases for which a statistically significant (at level 0.02) change in propagation with respect to reference interval occurred. The shade of the circles representing electrodes are proportional to the significant outflows in all directions for all subjects.

the cue) an increase of outflow was observed from several electrodes. The topography of this phenomenon is presented in Fig. 4, where a summary of the results for all subjects is illustrated. Only outflows surpassing the ones in the reference period are shown (significance level 0.02). The increased outflows occurred mainly at the electrodes at the midcentral area and at some electrodes located more frontally. For real finger movement this phenomenon has also been reported in Ginter and coauthors (2001).

Characteristics of gamma activity flows

The propagation of EEG activity during motor tasks is characterized by fast dynamics. In order to visualize its topography and time course we have constructed a program which presents such propagation in the form of a movie. The movies for the experiment as described in this paper are accessible on Internet (see

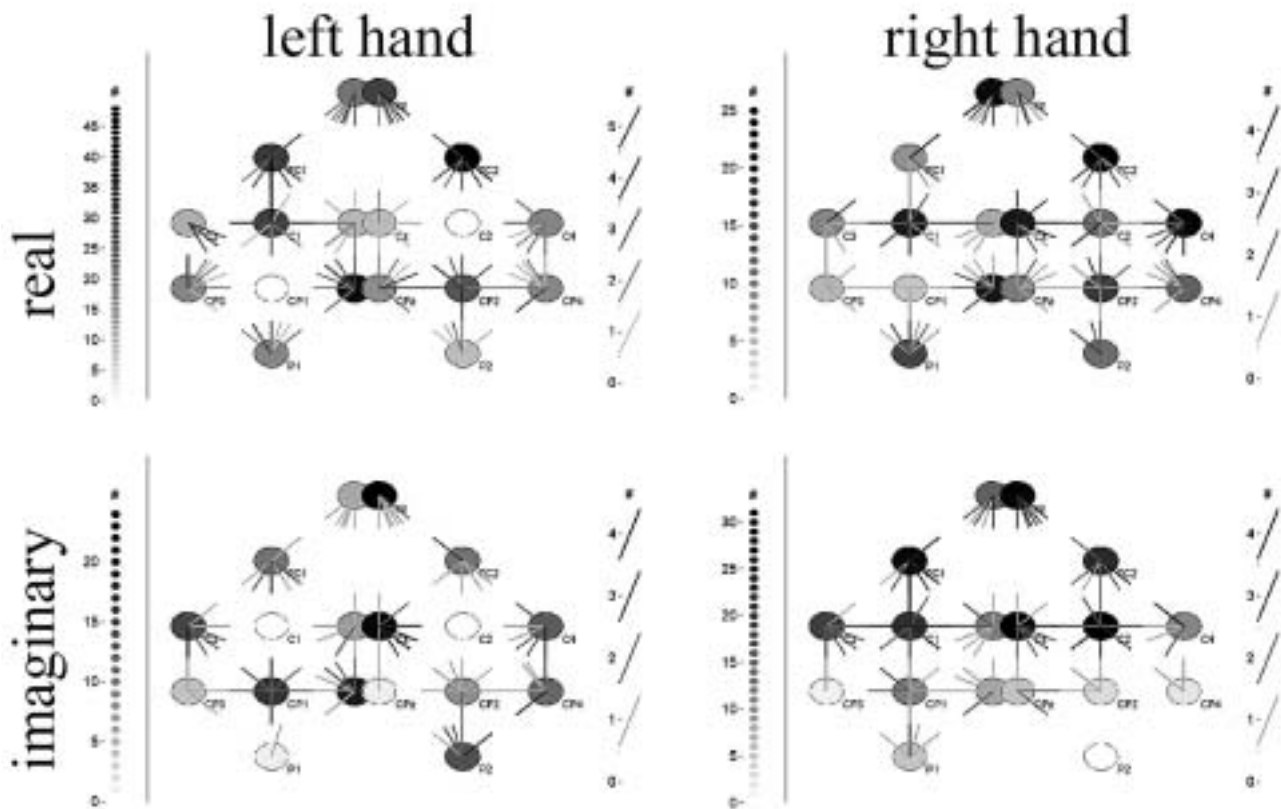


Fig. 4. Significant flows in the beta band after the motor task – the upper pictures for the real movement, lower pictures for the case of imagination. Pictures on the left correspond to the left hand, pictures on the right to the right hand. Presented are the flows, which differ significantly (at level 0.02) with respect to the reference interval in the three consecutive time windows. Convention of drawing as in Fig. 3.

http://brain.fuw.edu.pl/~kjbli/DTF_MOV.html). In Fig. 5, snapshots from the movie for one subject are shown.

In this figure the propagation in the gamma band, calculated as integrated values of SDTF in 35–41 Hz frequency band is illustrated in the form of the arrows. The characteristic differences between the real and imaginary movements illustrated in this picture include: (1) earlier appearance of propagation of gamma activity from C3 electrode in case of real movement (2) short duration of this phenomenon, (3) later occurrence of propagation from C3 in case of imagination, (4) longer period of activity for imagination task involving flows mainly from C3 and Cz.

For the real movement the burst of gamma activity appeared in the period 0.3–0.7 s (depending on the subject) after the cue presentation at the contralateral motor cortex areas (electrodes C1, C3 for right hand movement and C2, C4 for the left hand movement).

For the imagination task the gamma activity outflow always started later than for the real movement (for the case illustrated in Fig. 5 it was 1.0–1.1 after the cue onset) and bigger areas of the brain were engaged in activity emission, especially areas around electrodes Cz (this effect is visible at the lowest right picture of Fig. 5.)

In comparison with the real movement, in case of imagination, the propagation often started in more posterior areas – electrodes Cp1, Cp2, Cp3, Cp4 – which may be interpreted as bigger involvement of the sensory areas. In case of imagination of the left hand movement the gamma activity started to propagate in the right hemisphere (0.4–0.8 seconds after the cue onset), after which the flow was observed with a delay of about (0.7–0.8 seconds) in the symmetrical locations of the left hemisphere. For the right hand imagined movement the results were less consistent – in 5 cases out of 8 the flow started in the contralateral hemisphere.

Another characteristic feature of the real and imaginary tasks was the propagation from the central areas of the head, electrodes Cz, Fz, Fc1, Fc2, overlying the Supplementary Motor Area (SMA). For the right hand task especially propagation from Fc1 was observed and for the left hand task propagation from Fc2. The alternating flows from the primary motor cortex areas connected with finger movement and the areas overlying SMA were more pronounced for the case of imagination.

Summarizing these observations, in general terms we may say, that during the real movement a short signal in the gamma band concerning the performance of

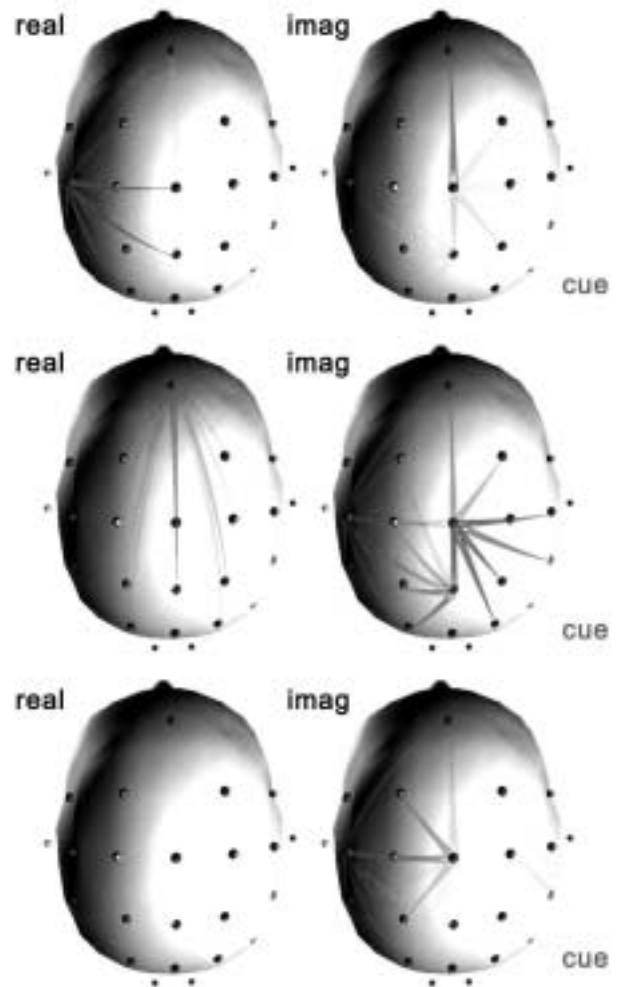


Fig. 5. Snapshots from the movie representing gamma activity propagation for one subject during the real (left column) and imaginary (right column) motor task for the right hand. Upper row – 0.3 s, middle row – 1.1 s, lower row – 1.4 s after cue presentation.

the task is emitted from the primary motor areas contralateral to the moving finger. In case of imagination the process is much longer and several structures of sensorimotor cortex are involved.

DISCUSSION

A main body of previous works concerning motor control was based on the analysis of EEG amplitude (Pfurtscheller and Lopes da Silva 1999), SDTF gives information about the phase difference between the signals recorded at different locations and hence about the propagation of the activity. Here we have determined for the first time the dynamic patterns of trans-

missions during movement and its imagination. New clues to the nature of the oscillatory neural mechanisms involved in motor control were provided, based on the observation of the cross-talk between distinct brain structures.

The patterns of propagation during motor task and its imagination bear resemblances such as the presence of the gap in propagation of beta activity during the task and preceding it burst of gamma from primary motor area. However, the pronounced differences were also observed: the gap in beta propagation was shorter and the propagation in gamma band lasted longer and involved more brain structures.

The phenomena observed by us such as decrease of propagation from sensorimotor areas in the beta band during the task and its increase afterwards correspond well with the event related desynchronization (ERD) and synchronization (ERS) described e.g. by Pfurtscheller and coauthors (2003), however the information contained in SDTF tells us not only about topographical localization, but also on transmission, elucidating the functional relations between structures.

The outflow from a certain location need not be exactly correlated with the EEG amplitude. The increase of outflow of beta activity before the right hand movement from locations around C1 electrode is not accompanied with an increase of amplitude of the beta rhythm in the corresponding locations. It may be interpreted in terms of information exchange between structures involved in motor action and an increase of the level of attention before the task. Beta rhythm has been connected with attention (Wróbel 2000). The smaller decrease of propagation in the beta band during imagination in comparison with the real movement may be explained as the need for higher concentration and a higher level of attention.

The beta propagation after the movement from the more frontal location with respect to the sensorimotor cortex (observed also in: Ginter et al. 2001) is in agreement with the results of an MEG experiment (Samelin and Hari 1994) indicating the existence of a source of beta activity in those areas.

Activity in the gamma band is very hard to observe in an EEG recorded by scalp electrodes, besides, it is often obscured by muscle artifacts. Usually, the gamma rhythm can be identified in a small fraction of the population only. In this study, however it was observed in all subjects. This was possible because of the unique properties of the SDTF function, which is

very robust in respect of noise and constant phase disturbances. SDTF is sensitive to phase differences between signals, so it allows us to extract phenomena connected with the shift of phase from a constant phase background – in this case a fast changing pattern of communication between brain structures in the gamma band.

The EEG activity of 40 Hz has been connected with focused arousal and motor programming (De France and Sheer 1998, Pfurtscheller et al. 1993, Salenius et al. 1996). The reported short increase of activity in the gamma band agrees with our observation of the brief increase of gamma propagation from the primary motor area connected with the finger movement.

Gamma outflow during imagination lasted much longer and involved larger areas of brain, which could have been expected. The evidence that movement imagery involves distributed cerebral sources is in agreement with the imaging studies indicating involvement of several brain areas connected with motor function (Neuper and Pfurtscheller 1999).

The propagation from more posterior locations with respect to the primary motor cortex observed by us for imagination may be explained in terms of bigger involvement of sensory areas. The enhanced activity in this region was found in the study of regional cerebral blood flow (Goldenberg et al. 1987). The role of SMA in the preparation of movement is well documented by functional magnetic resonance imaging (fMRI), e.g. Wildgruber and coauthors (1997), or Ball and colleagues (1999). The increased activity of SMA during the motor task was also found by means of cerebral blood flow (rCBF) and positron emission spectrography (PET) (reviewed by: Lang 1996). Strong coupling between SMA and the motor cortex was found in Thatcher and others (1994). The role of SMA in the imagination task was suggested in a paper by Deecke (1996) (concerning slow potentials) and in Neuper and Pfurtscheller (1999), Pfurtscheller and others (2003).

Our results give specific information concerning the mutual transmission in the gamma band between the locations overlying SMA and other sensorimotor areas, especially the primary motor area. In a motor imagery study by means of fMRI, changes in SMA, and to a minor extent in the premotor area, were found, but not in the primary motor area (Rao 1993). However, in other fMRI studies (e.g. Halett et al. 1994, Porro et al. 1996) some activation in the primary motor cortex during imagery was found. The discrepancy between

fMRI and EEG studies can be explained in view of our results, namely, during imagination we have found a decrease in propagation from the primary motor area connected with hand movement in the alpha and beta band, while the increase of propagation from that region concerned only the gamma band. Gamma activity involves small neural assemblies as suggested by Pfurtscheller and coauthors (2003), and is characterized by a small amplitude (Singer 1993), so it does not need to be connected with significant consumption of energy, therefore this activity may not be well reflected in fMRI. On the other hand, it plays an important role in the information processing in the brain.

CONCLUSIONS

In this paper we have presented for the first time the dynamically changing pattern of EEG activity propagation for real and imaginary movements which is consistent with our understanding of motor control. However, at the same time we have revealed novel observations concerning the transmission between the brain structures and their mutual interactions. The information gained by means of SDTF goes beyond the topographical localization of active structures, it gives the evidence about the cross-talk between the distinct sensorimotor areas.

Comparison of the activity flow during real and imaginary movement shows similarities in the pattern of propagation, however, there are also differences, especially in higher frequencies. In the case of imagination larger brain areas connected with motor control were involved, which was especially pronounced in case of gamma activity propagation.

Our results indicate the important role of the studies based not only on the overall activity of brain structures but on the specific role of the EEG rhythms, particularly gamma. The understanding of information processing by the brain requires topographically, temporarily and frequency selective estimators, which take into account the different functional roles of EEG rhythms. The SDTF method fulfills this requirement. The unique property of the method is the ability to extract very weak rhythmical activity, if it is characterized by the specific phase dependencies. Contrary to the bivariate methods for the estimation of directionality, SDTF gives consistent and physiologically meaningful pattern of interactions. This involves particularly the transmission of information between different

locations which may be connected with specific sensorimotor structures.

REFERENCES

- Andrew C, Pfurtscheller G (1999) Lack of bilateral coherence of post-movement central beta oscillation in the human electroencephalogram. *Neurosci Lett* 273: 89–92.
- Akaike H (1974) A new look at statistical model identification. *IEEE Trans Aut Contr* 19: 716–723.
- Ball T, Schreiber A, Feige B, Wagner M, Lucking CH, Kristeva-Feige R (1999) The role of higher-order motor areas in voluntary movement as revealed by high-resolution EEG and fMRI. *Neuroimage* 10: 682–694.
- Bernasconi C, König P (1999) On the directionality of cortical interactions studied by structural analysis of electrophysiological recordings. *Biol Cybern* 81: 199–210.
- Blinowska KJ, Kuś R, Kamiński M (2004) Granger causality and information flow in multivariate processes. *Phys Rev E* 70: 050902.
- Bressler SL (1990) The gamma wave: A cortical information carrier? *Trends Neurosci* 13: 161–162.
- Buser P, Rougeul-Buser A (1995) Do cortical and thalamic bioelectric oscillations have a functional role? A brief survey and discussion. *J Physiol Paris* 89: 249–254.
- Crone NE, Miglioretti DL, Gordon B, Lesser RP (1998) Functional mapping of human sensorimotor cortex with electrocorticographic spectral analysis II: Event-related synchronization in the gamma band. *Brain* 121: 2301–2315.
- Deecke L (1996) Planning, preparation, execution and imagery of volitional action. *Cognitive Brain Res* 3: 59–64.
- De France J, Sheer DE (1998) Focused arousal, 40-Hz EEG and motor programming. In: *The EEG of Mental Activities* (Giannitrapani G, Murri L, eds). Karger, Basel, pp 153–168.
- Ding M, Bressler SL, Yang W, Liang H (2000) Short-window spectral analysis of cortical event-related potentials by adaptive multivariate autoregressive modeling: Data preprocessing, model validation, and variability assessment. *Biol Cybern* 83: 35–45.
- Efron B (1979) Bootstrap methods: Another look at the jackknife. *Ann Stat* 7: 1–26.
- Franaszczuk PJ, Blinowska KJ, Kowalczyk M (1985) The application of parametric multichannel spectral estimates in the study of electrical brain activity. *Biol Cybern* 51: 239–247.

- Franaszczuk PJ, Bergey GK (1998) Application of the directed transfer function method to mesial and lateral onset temporal lobe seizures. *Brain Topogr* 11: 3–21.
- Freiwald WA, Valdes P, Bosch J, Biscay R, Jimenez JC, Rodriguez LM, Rodriguez V, Kreiter AK, Singer W (1999) Testing non-linearity and directedness of interactions between neural groups in the macaque inferotemporal cortex. *J Neurosci Meth* 94: 105–119.
- Ginter J Jr, Blinowska KJ, Kamiński M, Durka PJ (2001) Phase and amplitude analysis in time-frequency space – application to voluntary finger movement. *J Neurosci Methods* 110: 113–124.
- Ginter J Jr, Blinowska KJ, Kamiński M, Durka PJ, Pfurtscheller G, Neuper C (2005) Propagation of EEG Activity in the Beta and Gamma Band during Movement Imagery in humans. *Methods Inf Med* 44: 106–113.
- Goldenberg G, Podreka I, Steiner M, Willmess K (1987) Patterns of regional cerebral blood flow related to memorizing of high and low imagery words: An emission computer tomography study. *Neuropsychologia* 25: 473–485.
- Granger CWJ (1969) Investigating causal relations by econometric models and cross-spectral methods. *Econometrica* 37: 424–438.
- Gross J, Timmermann L, Kujala J, Dirks M, Schmitz F, Salmelin R, Schnitzler A (2002) The neural basis of intermittent motor control in humans. *Proc Natl Acad Sci U S A* 99: 2299–2302.
- Hallet M, Fieldman J, Cohen LG, Sadato N, Pascual-Leone A (1994) Involvement of primary motor cortex in motor imagery and mental practice. *Behav Brain Sci* 17: 210.
- Inouye T, Iyama A, Shinosaki K, Toi S, Matsumoto Y (1995) Inter-site EEG relationships before widespread epileptiform discharges. *Int J Psychophysiol* 82: 143–153.
- Kamiński M, Blinowska KJ (1991) A new method of the description of the information flow in the brain structures. *Biol Cybern* 65: 203–210.
- Kamiński M, Blinowska KJ, Szelenberger W (1997) Topographic analysis of coherence and propagation of EEG activity during sleep and wakefulness. *Electroenceph Clin Neurophysiol* 102: 216–227.
- Kamiński M, Ding M, Truccolo W, Bressler S (2001) Evaluating causal relations in neural systems: Granger causality, directed transfer function and statistical assessment of significance. *Biol Cybern* 85: 145–157.
- Kamiński M, Liang H (2005) Casual Influence: Advances in Neurological Analysis. *Crit Rev Bioeng* 33: 347–430.
- Korzeniewska A, Kasicki S, Kamiński M, Blinowska KJ (1997) Information flow between hippocampus and related structures during various types of rat's behavior. *J Neurosci Meth* 73: 49–60.
- Kopell N, Ermentrout GB, Whittington MA, Traub D (2000) Gamma rhythms and beta rhythms have different synchronization properties. *Proc Natl Acad Sci U S A* 97: 1867–1872.
- Kuś R, Kamiński M, Blinowska KJ (2004) Determination of EEG activity propagation: Pair-wise versus multichannel estimate. *IEEE Trans Biomed Eng* 51: 1501–1510.
- Lang W, Cheyne D, Höllinger P, Gerschlagler W, Lindinger G (1996) Electric and magnetic fields of the brain accompanying internal simulation of movement. *Brain Res Cogn Brain Res* 3: 125–129.
- Lopes da Silva FH (1992) The rhythmic slow activity (theta) of the limbic cortex: An oscillation in search of a function. In: *Induced Rhythms in the Brain* (Başar E, Bullock TH, eds). Birkhäuser, Boston, pp 83–102.
- Marple LS Jr (1987) *Digital Spectral Analysis with Applications*. Prentice Hall, Englewood Cliffs, NJ.
- Neuper C, Pfurtscheller G (1999) Motor imagery and ERD. In: *Event-Related Desynchronization, Handbook of Electroencephalography and Clinical Neurophysiology*. Revised Edition, Vol. 6 (Pfurtscheller G, Lopes da Silva FH, eds). Elsevier, Amsterdam, pp 303–325.
- Pfurtscheller G, Neuper Ch, Kalcher J (1993) 40-Hz oscillations during motor behavior in man. *Neurosci Lett* 62: 179–182.
- Pfurtscheller G, Lopes da Silva FH (eds) (1999) *Event-Related Desynchronization, Handbook of Electroencephalography and Clinical Neurophysiology*, Revised Edition, Vol. 6. Elsevier, Amsterdam, pp 303–325.
- Pfurtscheller G, Graimann B, Huggins JE, Levine SP, Schuh LA (2003) Spatiotemporal patterns of beta desynchronization and gamma synchronization in corticographic data during self-paced movement. *Neurophysiol Clin* 114: 1226–1236.
- Porro CA, Francescato MP, Cettolo V, Diamond ME, Baraldi P, Zuiani C, Bazzocchi M, di Prampero PE (1996) Primary motor and sensory cortex activation during motor performance and motor imagery: A functional magnetic resonance imaging study. *J Neurosci* 16: 7688–7698.
- Rao SM, Binder JR, Bandettini PA, Hammeke TA, Yetkin FZ, Jesmanowicz A, Lisk LM, Morris GL, Mueller WM, Estkowski LD, Wong EC, Haughton VM, Hyde JS (1993) Functional magnetic resonance imaging of complex human movements. *Neurology* 43: 118–136.

- Saito Y, Harashima H (1981) Tracking of information within multichannel record: Causal analysis in EEG. In: *Recent Advances in EEG and EMG Data Processing* (Yamaguchi N, Fujisawa K, eds). Elsevier, Amsterdam, pp 133–146.
- Salenius S, Salmelin R, Neuper C, Pfurtscheller G, Hari R (1996) Human cortical 40 Hz rhythm is closely related to EMG rhythmicity. *Neurosci Lett* 213: 75–78.
- Salmelin R, Hari R (1994) Spatiotemporal characteristics of sensorimotor neuromagnetic rhythms related to thumb movement. *Neuroscience* 60: 537–550.
- Singer W (1993) Synchronization of cortical activity and its putative role in information processing and learning. *Ann Rev Physiol* 55: 349–74.
- Singer W, Gray CM (1995) Visual feature integration and the temporal correlation hypothesis. *Ann Rev Neurosci* 18: 555–586.
- Thatcher RW, Toro C, Pfielger ME, Hallet M (1994) Human neural network dynamics using multimodal registration of EEG, PET and MRI. In: *Functional Neuroimaging* (Thatcher RW, Hallet M, Zeffiro T, John ER, Huerta M, eds). Academic Press, pp 269–278.
- Wildgruber D, Erb M, Klose U, Grodd W (1997) Sequential activation of supplementary motor area and primary motor cortex during self-paced finger movement in human evaluated by functional MRI. *Neurosci Lett* 227: 161–164.
- Wróbel A (2000) Beta activity: A carrier for visual attention. *Acta Neurobiol Exp (Wars)* 60: 247–260.

Received 18 May 2006, accepted 11 October 2006