Cortical connectivity during word association search

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Received 5 October 1999; received in revised form 18 September 2000; accepted 7 February 2001

Abstract

Cortical connectivity was studied in tasks of generating the use of words in comparison with reading aloud the same words. These tasks were used earlier in PET and high density ERP recordings studies (Posner and Raichle, 1997; Abdullaev and Posner, 1998), in which both the functional anatomy and the time course of cortical areas involved in word processing were described. The wavelet transforms of ERP records and the calculation of correlations between wavelet curves were used to reveal connections between cortical areas. Three stages of intracortical communications while task performance were found. These were: (1) the connections between right and left frontal and central areas which preceded stimulus delivery and persisted up to 180 ms after it; (2) the network connecting right and left frontal with left posterior temporal–parietal junction at 280–450 ms; and (3) communications between left and right temporal zones in 550–800 ms. The data are in good agreement with results of previous PET and ERP studies and supply the earlier findings with circuitry of cortical information transfer. © 2001 Published by Elsevier Science B.V.

Keywords: Binding problem; Thinking; Language; Word association; EEG mapping; Wavelet transforms

1. Introduction

Recent experiments using brain imaging methods such as positron-emission tomography, functional magnetic resonance and high density electroencephalographic potential recording enabled to reveal basic cortical areas activated in verbal thinking. It was shown that definite mental operations, as described by cognitive psychology, could be attributed to particular cortical areas (Posner and Raichle, 1997). The above-mentioned approaches, however, could supply the experimenter with only indirect information of how these areas communicate with each other and what is indeed the design of cortical circuits participating in word
analysis. This problem, i.e. the binding problem, is, however, very important for understanding the brain mechanisms underlying higher brain functions as mental activity emerges indeed in result of complicated brain structures interaction.

One of the perspective approaches to explore the problem of cortical connectivity is based on the idea that cortical communications are promoted by the concordance in the rhythmical properties of the interacting neuronal ensembles, manifested particularly in their electrical potentials synchronization (Livanov, 1972, 1986). This idea, ascending to some fundamental approaches of the Russian neurophysiological school (Ukhtomsky, 1936/1951) was confirmed later both in experimental studies of the cortical connectivity in humans (Thatcher et al., 1986; Gevins et al., 1990; Petsche and Rappelsberger, 1992; Bullock et al., 1995; Srinivasan et al., 1999) and in studies using mathematical modeling of neural processes (v.d. Malsburg and von der Schneider, 1986; Abarbanel et al., 1996).

The theoretical background for this approach is the fact, that when two or several neuronal groups have equal (or close) oscillation frequency, the signals from one neuronal group reach another group repeatedly in the same phase of the excitation cycle. If this phase is the exaltatory one, excitation threshold of the second neuronal group appears to be of the minimal value, promoting its involvement in the concerted with the first group activity. Following this logic, not only frequency parameters of the communicating groups have to be the same, but also the phase shift should be constant during the neuronal message transmission.

This condition is perfectly met by coherence function and, therefore, the coherence analysis, beginning from Livanov’s experiments, is considered as the most adequate for the binding problem exploration. This approach made indeed a most important contribution in studying brain connectivity. The efficiency of this experimental tool was increased when the methods for coherence analysis in short time intervals were elaborated (Gersch, 1987; Florian et al., 1998), up to instantaneous evaluation of the coherence function (Schack et al., 1999a,b).

Still the design of neural communication can be even more complicated than that described by coherence function. Each of communicating neuronal groups can alternately send and receive the neural messages. This process is controlled with phase shift mechanism, influenced, e.g. by the third group. When the phase of the excitation cycle is changed from the exaltatory to the refractory one, the group stops the message reception and in appropriate phase relationship begins to send its own massage — a kind a neural answer to just received information. It is noticeable, that the phase changes in both groups are not synchronous in this case. The constant phase shift — the main condition for coherence — is maintained indeed only during the active impulse trains transmission. One may suppose, however, that this parameter can be changed repeatedly even inside the elementary mental operation.

Furthermore, the transient phase shift itself can be the information carrier. Thus, according to Hoppensteadt and Izhikevich (1996a,b), information in neural message can be encoded in phase shifts, as it takes place in FM radio signal. The authors supposed that such phase shifts are the part of memory mechanism.

Shaw (1984) evidenced that if the rhythmic oscillations of the same frequency do not coincide in time (what is the fact in ‘dialogue’ activity) the coherence falls to zero. Bullock et al. (1995) declared that coherence analysis being the valuable tool in connectivity studies in some cases could give, however, the false results. Therefore, when exclusively the common coherence analysis is applied in the study of brain connectivity, the part of connections could be omitted. These critical points relate indeed to the common, but not to the instantaneous coherence analysis (Schack et al., 1999a,b).

But still it is reasonable to use also another, more liberal criterion in study of cortical communications. Such criterion of the universal value is the coincidence of the frequency parameter in the distant neuronal groups. From this viewpoint the phase relationship is a secondary variable, which can be neglected while studying the whole design of cortical networks underlying mental functions and consisting both of excitatory and
inhibitory, active and potential cortical connections of the alternate direction.

This idea was realized in the method named ‘intracortical interaction mapping (IIM)’ (Ivanitsky, 1990, 1993; Ivanitsky et al., 1999). IIM is based on three theoretical premises:

1. Neuronal groups in the cortex have functional specialization. This proposition has been supported by the PET and fMRI studies.

2. The neurons within the group are connected by direct and backward connections in such a way that the group acquires the feature of the neuronal oscillator (Kasanovich and Borisyuk, 1995; Konig and Schillen, 1991; Basar and Schuermann, 1996).

3. The precise coincidence of neuronal oscillators frequency parameters promotes the establishment of the connections between them.

Using this method, the patterns of cortical connections specific for particular types of cognitive activity such as imaginary, spatial and verbal thinking were described (Ivanitsky and Ilyuchenok, 1992; Sidorova and Kostyunina, 1991; Nikolaev et al., 1996; Ivanitsky, 1999).

The present study describes the picture of cortical connections in a verbal task. Our particular aim was to synthesize two approaches, that based on multi-electrode event-related potentials (ERP) recording resulted in detection of the cortical areas involved in word processing as well as the time course of their activation and that revealing the cortical connectivity during this task performance. For this purpose the results of experiments carried out by Abdullaev and Posner (1997, 1998) in the Department of Psychology, University of Oregon in Eugene were sent to the Institute of Higher Nervous Activity and Neurophysiology in Moscow. The data sent were 64 channel ERP records made during experiment in which the subjects were asked either only to read aloud the words that appeared on the monitor screen or to generate their use. The tasks of reading and use-generation have been well studied from a cognitive and anatomical viewpoint, so we considered them to be the ideal ones for our purposes. Abdullaev and Posner (1998) found the following areas of activation while use-generation task performance: anterior cingulate at approximately 150 ms; left frontal and occipital at approximately 200 ms; left posterior approximately 600 ms; and right insula at 800–1100 ms.

Fig. 1 depicts the electrode arrangement in this study. The cortical regions, where ERP amplitude revealed statistically significant difference in use-generation task as compared to reading aloud task are marked. The same areas (plus the cerebellum) have also been active during PET studies (Raichle et al., 1994; Posner and Raichle, 1997). The results of the further data processing in Moscow are the item of this paper.

2. Method

2.1. Subjects

The experiment was conducted at the University of Oregon and involved 21 right handed subjects (14 females, seven males), aged from 18 to 33, handiness defined by Edinburgh handiness inventory (Oldfield, 1971; Raczkowski et al., 1974).

2.2. Task

Single nouns were tachistoscopically presented (150 ms on time) on a monitor screen. No noun was presented more than once. After 750 ms (900 ms after stimulus onset) a question mark appeared for 150 ms and served as a response cue to prompt the subject’s response. The subject either pronounced the presented word (reading aloud condition), or supplied a semantically-related verb, e.g. hammer → pound (use-generation condition). The random intervals of 2–5 s were used between noun presentations. The subject had to perform 120 tasks of each type. Before recording, each subject rehearsed the task with 10–20 practice trials with a different set of words.

2.3. EEG recording

EEG was recorded from 64 channels using a right ear mastoid as reference. The electrode positions and names are depicted in Fig. 1. The
Fig. 1. The electrode positions and names that were used according to extended International 10-20 System. Cortical regions, in which the ERP in use-generation and reading aloud conditions was significantly different in the experiments by Abdullaev and Posner, 1998, are shaded. The shadow density depicts the approximate delay, at which the significant difference occurred. The difference between use-generation and reading aloud ERPs was positive in most cases, with the exception of early posterior and late temporal and frontal ERPs, where this difference was negative.

The trials with muscle, eye movement and other kinds of artifact were excluded from further ana-
Analysis using the combined method of automatic data rejection and visual inspection. The criteria for artifact rejection were in general more strict than in the original study by Abdullaev and Posner (1998) and, therefore, the trials selected for further analysis were somewhat different from those used in their paper. Such strict selection was necessary as the artifact can severely deteriorate the EEG spectra. Before beginning the artifact elimination procedure, the EEG records were ‘unscrewed’. This means that the possible inclination of the records against the zero line was eliminated. It was made via calculating the average slope of the record by means of linear regression and then subtracting this slope from the record. The artifact elimination procedure was applied to the data of each subject separately and consisted of two passes. During the first pass, the channels whose records were consistently contaminated with artifacts were detected and declared as ‘bad’ channels. These ‘bad’ channels were then completely excluded from the analysis of the given subject’s data. During the second pass, the trials that contained artifacts in other channels (not those previously detected as ‘bad’) were discarded. The goal of the first pass was to find and eliminate channels that were systematically affected by artifact-causing circumstances, such as bad electrode attachment or sustained muscle tension. We found it reasonable not to use the data recorded from these channels at all. The goal of the second pass was to discard trials that had occasional artifacts in other channels.

In more detail, the procedure looked as follows. During the first pass, any single-channel record was marked as containing artifact if: (a) the recorded signal exceeded the threshold of ±50 μV or ±3 S.D. of the mean amplitude, whichever was less; or (2) the signal changed for more than 50 μV or 3 S.D. within the time interval of 8 ms; or (3) the spectral power of the record looked like a high-amplitude chopper in the range 25–40 Hz (this was visually detected). Then, if for the given channel the artifacts were found in more than 50% of trials, the whole channel was declared as ‘bad’ for the given subject. During the second pass, a record was marked as containing artifact if either: (a) the signal exceeded the threshold of ±5 S.D. of the mean amplitude; or (2) the signal changed for more than 3 S.D. within the time interval of 8 ms. Then the trials that contained artifacts in ‘not bad’ channels were discarded.

After finishing these steps one more thing was done, the records that violated the absolute or relative threshold condition in the second pass of the procedure were visually inspected for the presence of the high-amplitude alpha-rhythm and if the threshold violation was merely due to this reason, those records were recuperated.

2.5. Data processing

The general algorithm of the search for cortical connections basing on the approaches described in the introduction was as follows. First, we had to pick up transient rhythms from single-channel records. Then we had to introduce a measure of how much the thus found rhythms coincide in time and frequency in different EEG channels. Finally, we needed to evaluate statistically whether the coincidences (if any) were consistent and repetitive. Since we compared two mental conditions (use-generation vs. reading aloud) it seemed reasonable to follow the differential approach and to compare statistically the measure of coincidence in two mental conditions. This gave us the knowledge of what coincidences appeared additionally in one condition compared to the other.

As soon as we speak approximately transient rhythms that are related to the external events, we must distinguish between at least two types of them. The first type is represented by rhythms time and phase locked to the stimulus. These rhythms are frequently called evoked rhythms (Basar et al., 1992; Tallon-Boudry et al., 1996) and are interpreted as being concerned with the ascending processing of information in the brain, from sensory input to higher cortical levels (the so called ‘bottom-up’ processing). The rhythms of the second type are not phase-locked to the external event and are understood as being pertinent to endogenous cortical processes. These latter rhythms are frequently called the induced rhythms.
In the present study we analyzed both types of rhythms. To draw out the evoked rhythms, we made averaging of single trials in time domain. There were certain reasons to utilize this approach. Firstly, the analyzed time intervals were rather short and in this short time intervals the processes triggered by the external stimulus could be dominant. Secondly, the averaging enhanced the activity that was specific for given task performance and rejected the ‘cerebral noise’, i.e. contribution of the cortical oscillators not involved directly in this specific activity to surface EEG. Moreover, we attempted to relate the results of time-frequency analysis to results of the average ERP study, which was performed on the same data by Abdullaev and Posner (1997, 1998).

When analyzing the induced rhythms, the primary time-frequency analysis was applied directly to single ERP trials. In this case the information on the fine time-phase structure of the rhythms was lost at the initial stage of the processing and not only phase locked to the stimulus were revealed.

One of the mathematical methods that allow localizing rhythmic trains in time and frequency domains simultaneously is a wavelet transform (WT). A WT of a signal that is a function of time (e.g. a single-channel EEG record) is obtained by convolving the original signal with a template — a short complex-valued oscillating signal, the so-called ‘mother wavelet’. By dilating or compressing the mother wavelet it is possible to calculate the WT curve for any given frequency. This curve shows the time course of the energy envelope of this frequency rhythmic component in the original signal, the information on the fine time-phase structure of the input signal is lost at this moment. A family of WT curves calculated for different frequencies forms a surface defined on a time-frequency plane. This surface depicts a two-dimensional energy envelope of the original signal’s rhythmic components and shows how these components vary in time and frequency. The more detailed review of WT theory and its application is given by Torrence and Compo (1998).

In our previous studies with IIM method (Ivanitsky et al., 1999), we used the Fourier Transform as a basic method for EEG spectral analysis. In those studies we had long (of few seconds duration) time intervals, during which the subject persistently solved a complicated mental task performing, perhaps, a certain set of mental operations in a different order and in arbitrary time moments. We were interested in revealing the frequency structure of the EEG signal, which reflected, according to our notion, those operations and not so much in disclosing the time course of the rhythmic components since this course was anyway different in different trials. In the present study, the tasks were short and the subject performed a certain sequence of mental operations each time he (or she) solved them. The goal of this study was to find the electrophysiological evidence for such a sequence in terms of brain rhythms, so we needed the investigation method that could supply us with both time and frequency analysis simultaneously. This was the reason why in this study we preferred the WT before the Fourier transforms.

Our goal was then to find time intervals, in which the time courses of two WT curves coincided, i.e. the curves went similarly. So, we calculated the correlation coefficient (CC) between two WT curves of a channel pair inside a sliding window of certain duration. A high value of CC demonstrates that the rhythms of the considered frequency appeared (and disappeared) in this time interval simultaneously in both channels (Fig. 2.).

In accordance with previous description, two types of processing were applied to the data: (1) calculating the average ERPs, then making the WT and then finding the CCs, while investigating the evoked rhythms; and (2) applying WT to single EEG trials, then finding CCs and then averaging them, while investigating the induced rhythms. The first type of processing is abbreviated to AWC (‘Averaging-Wavelet-Correlations’) and the second type, to WCA (‘Wavelet-Correlations-Averaging’).

As we followed the differential approach, we compared the CCs between two conditions (usage-generation vs. reading aloud) using a statistical test for this purpose, with data sets varying across subjects. As we had multiple comparisons, we faced the problem of false positive results. To avoid this problem, we applied additional filtra-
Fig. 2. The figure illustrates a principle of the method. WT curves for 45 Hz averaged across subjects in channels 25, 38, 39 and 40 in reading aloud (a) and use-generation (b) tasks are shown. Note that approximately 200 ms the curves in reading aloud become highly correlated for approximately 100 ms, but no such a correlation in use-generation is observed. The vertical line marks a moment of maximal energy of 45 Hz frequency component in channel 38. In use-generation the curves in the correspondent time window go discordantly, and hence, the correlation coefficients are low.
tion of results in time and frequency domains, as described below.

2.6. Procedure

1. The average ERPs for different mental conditions were calculated for each subject separately in evoked rhythms study (AWC). In induced rhythms study (WCA) this was not done and single EEG trials were subjected to the next step of processing directly.

2. The WT curves using the Morlet mother wavelet were calculated for frequencies 9, 10, 11, 12, 13, 15, 16, 17, 19, 21, 22, 24, 27, 29, 32, 35, 38, 41 and 45 Hz for either average ERPs or single EEG trials. The frequency step increased with increasing frequency since the frequency resolution of WT decreases with frequency. Theta-rhythm was not analyzed since EEG records of 1 s duration were considered to be too short to analyze frequencies below 8 Hz.

3. In total 64 channels were recorded, but six of them (LinfOrb, RinfOrb, Nasion, LoutCan, RoutCan, Lmast) were not EEG channels. Fifty-eight channels formed 1653 pairs. For every subject, every mental condition, every electrode pair and every frequency the CC between two WT curves was calculated in a time window of 184 ms duration moving along the time axis with 92 ms steps (184 ms was the duration of the pre-stimulus interval and all windows were of the same duration). Thus, 10 values of cross-channel CC were obtained for each of the above-mentioned combinations of subject, mental condition, electrode pair and frequency.

4. In the induced rhythms study (WCA) the CCs were averaged separately for each subject and mental condition.

5. The CCs obtained in reading aloud and use-generation conditions were compared using the matched pairs signed ranks Wilcoxon test for every time window, electrode pair and frequency. To avoid false positive results, which could be the consequence of multiple comparisons, we used the following approach. We believe that the phenomena observed in partly overlapped time windows and neighboring frequencies should be dependent in case they reflect a certain physiological process and not — if they are observed by chance. So, the only differences in CCs were considered as really significant, for which Wilcoxon test showed the significance level $P < 0.05$ simultaneously in two neighboring time windows and in two adjacent frequencies. The thus selected combinations of time interval and frequency were further treated as cortical connections, according to our ideology (see Section 1) and named so.

6. Still, the further reduction of results was done. The total number of connections across all pairs was calculated for each combination of time window and frequency. Only those windows/frequencies, for which the number of connections exceeded the level of 2 S.D. of mean number of connections, were selected. Finally, only those connections were further considered, which resided in the thus selected window/frequency cells. We believe that this rather severe reduction of data minimized the number of coincidences found by chance.

3. Results

The first remarkable result was the close topographic distribution of connections revealed by above-mentioned way. As one can see on Figs. 3 and 5 the most obtained connections, they have at least one common electrode or link the electrodes located in neighboring sites forming thus ‘the bundles’ of connections. This fact emphasizes a non-random character of obtained results and proves a reliability of the method.

According to the principles described in the previous section of the paper, five connection networks were found for use-generation task, two based on induced and three on evoked rhythms. Also five networks (three for induced and two for evoked rhythms) characterized reading aloud task.
Fig. 3. Cortical connections that appeared additionally in use-generation task as compared with reading aloud task in the selected windows/frequencies, for which the number of connections exceeded the level of 2 S.D. of mean number of connections. (a) WCA networks, (b) AWC networks. The lines connect cortical sites in which WT curves correlated significantly higher in use-generation task than in reading aloud task.
3.1. Use-generation task

The maps of cortical connections in use-generation tasks are presented in Fig. 3. The first figure depicts the networks based on induced and the second one, on evoked rhythms, i.e. for results got with WCA and AWC data processing, respectively.

3.1.1. WCA networks

The first network maintained on 38 Hz frequency consisted of multiple connections located predominantly in right and left frontal areas. It covered the time interval practically from the onset of the record to 184 ms after word presentation. The second network was based on 29 Hz rhythm and was manifested in time window from 93 to 276 ms after stimulus. It consisted of several short connections located predominantly in right frontal areas and a number of longer diagonal connections.

3.1.2. AWC networks

These networks appeared later than WCA networks. The first of them based on 22 Hz frequency oscillations was manifested in time window from 277 to 460 ms. It consisted of the bundle of connections binding right and left frontal areas with left temporal–parietal zone. The second network of 41 Hz connections covered the time window 461–644 ms and was located in right frontal zone. The third network (35 Hz, 553–736 ms) consisted of rather long transversal connections binding right and left temporal–parietal areas.

Fig. 4. Mean correlation coefficients in use-generation and reading corresponded to the maps in the Fig. 3 (higher in use-generation). (a) WCA networks, (b) AWC networks. On the time scale the middle of time windows are indicated. The solid points mark the moments of maximal difference. The whiskers are ±S.E.M. The S.E.M.s are higher for WCA networks, in which WT was applied to single EEG trials, than for AWC. Note that the statistically significant differences were calculated for CCs in each electrode pair, but not for averaged CC in the network.
Fig. 5. Cortical connections that appeared additionally in reading aloud task as compared with use-generation task. All designations are the same as on the Fig. 3.
3.1.3. Correlation coefficients curves

The mean CCs for above mentioned windows/frequencies are shown in Fig. 4. Fig. 4a represents the dynamics of CCs for two WCA networks. For 35-Hz network, the difference reached its maximum at zero point of time scale, i.e. at the moment of stimulus presentation. For the second 29-Hz network, the maximal difference was at 184 ms. Fig. 4b depicts CCs for three AWC networks. These networks were maintained on 35 Hz (maximal difference at 644 ms), 22 Hz (maximal difference at 368 ms) and 41 Hz (maximum at 552 ms).

The important feature of all of these curves was that the maximal difference, which corresponded also to the level of statistical significance, was reached due to the opposite direction shifts of the CC curves in use-generation and reading aloud conditions. In all three AWC networks, the correlation coefficient in reading fell below zero at the difference peak.

3.2. Reading aloud task

Five networks found in reading aloud task are presented in Fig. 5. The first depicts the WCA and the second AWC connections.

3.2.1. WCA networks

The general feature of all WCA networks was that they consisted of numerous connections located mostly in posterior and central and reached only few points in frontal cortical areas. The first network was built by of the system of connections based on 21 Hz rhythm in time window from the beginning of the record to 92 ms after the stimulus presentation. The second one was the network of 16 Hz connections functioning from 277 to 460 ms after word presentation. The third network was a biggest one and consisted of the system of multiple 29 Hz connections in next time window of 369–552 ms.

3.2.2. AWC networks

The first network based on 22 Hz rhythm appeared in time window 0–184 ms and was located predominantly in right posterior cortical quadrant. Another network of 41 Hz connections (185–368 ms) was rather widespread, but as in the WCA networks, only solitary connections reached the frontal cortical area. It is remarkable that two of these networks were maintained on the same frequencies (22 and 41 Hz) as the AWC connection systems in use-generation task.

3.2.3. Correlation coefficients curves

The curves of the mean CCs for all five networks described above are presented in Fig. 6a (WCA networks) and Fig. 6b (AWC networks). WCA networks are that based on 21 Hz (peak difference at zero point), 16 Hz (368 ms) and 29 Hz (460 ms). AWC networks were the connection systems based on 22 Hz (92 ms) and 41 Hz (276 ms). As in the situation of use-generation task, the maximal, statistically significant difference between correlation coefficients in two tasks was reached due to concordant, but directed to opposite sides curves shifts, the CCs increased in reading while diminished in use-generation. However, here the CCs values were never negative.

4. Discussion

The general aim of this study was to supply the anatomy of the cortical regions involved in the word association process with the picture of cortical communications. These communications integrate activated cortical areas in a whole system, which performs the search of associating word. Quite independent approaches were used in the studies of the active cortical zones and cortical connectivity. Therefore, both the coincidence and non-coincidence, the new data with the former ones may be expected. It means that cortical connections may or may not be of between the ‘regions of interest’ (the term accepted in brain imaging researches) revealed in previous PET (Raichle et al., 1994; Posner and Raichle, 1997) or high density ERP studies (Abdullaev and Posner, 1997, 1998). The results, presented in this paper, show that connectivity data are, in general, in good agreement with that got by other methods. This agreement concerns both the anatomy of communicating areas and the time course of their activation. One may note, however, that the
Fig. 6. Mean correlation coefficients in use-generation and reading corresponded to the maps in the Fig. 5 (higher in reading). All designations are the same as in Fig. 4.
connectivity networks appeared, as a rule, earlier than the activation of the appropriate cortical areas as revealed with ERP study. This fact can be easily understood as the information transmission actually initiates brain structure activation and, therefore, should precede it. This compatibility of the results is remarkable as it provides the independent verification of the whole amount of data. It is especially important for this study, which used a new method to reveal cortical connectivity during particular cognitive verbal operations.

The principal question is, however, what our study adds to understanding the mechanisms of verbal thinking. There are two items where spectral analysis can supply the experimenter with new facts. These are the frequency coding of brain processing and the cortical connectivity patterns. It is also possible, analyzing induced and evoked rhythms, to distinguish brain processes, which are mostly of endogenous origin, from that triggered by external stimulus.

The cortical networks revealed in this study are based on the high-frequency part of EEG rhythms, beta and gamma. Gamma oscillations, as shown in studies by Llinas and Ribary (1992) promote cortical areas co-operation and provide the optimal conditions for specific informational processing. It was reported also that gamma waves participate in visual image integration (Singer and Gray, 1995; Schuermann et al., 1997). An important role of gamma rhythms in word information analysis was shown (Lutzenberger et al., 1997; Pulvermüller, 1999).

The ‘frequency of interest’ in cortical communications is also the beta rhythm. Recent studies (Whittington et al., 1997) declare that beta oscillations can be originated from gamma ones. Particularly this occurs when two neuronal ensembles are interconnected. The gamma-to-beta switching appears in result of spike doublets, which produce prolonged excitatory and inhibitory phases of excitation cycle. EPSP in this case increases, and the authors propose that this process be followed by the long-term potentiation, which is a part of the memory mechanisms.

In our previous studies (Nikolaev et al., 1996; Ivanitsky, 1999) it was also shown, that the architecture of beta connections is most specific to the type of thinking operation. The important role of beta rhythms in word processing was also found by Schack et al. (1999a, b).

There is one more problem, when gamma oscillations are studied in scalp EEG. In fact, not only brain but muscle activity may contribute in high frequency bands. As was said earlier, to eliminate these artifacts we carefully inspected all EEG trials and excluded those of them, which had flat spectral increase in 20–40 Hz simultaneously in few channels. Moreover, our results scarcely could be explained by muscle activity, because one may expect that it effect more the EEG signals in more difficult (use-generation) tasks. This difficulty should be reflected by the high frequency power increase simultaneously in many (mostly lateral) electrodes in the broad spectrum range (Pulvermüller et al., 1997) that could be resulted in the increase of false connections between appropriate cortical areas. However, in our studies the greater number of connections in gamma band was found in simpler (reading) task. Furthermore, the connections were based on the same particular frequencies in use-generation and reading aloud tasks, but had quite different location. Therefore, the assumption on the possible artifact origin of these connections is scarcely probable.

Three basic blocks of connections can be distinguished in use-generation task. These are earlier one, beginning before the stimulus presentation and up to approximately 250 ms after the stimulus, then the intermediate (280–450 ms) and the late (550–800 ms) blocks. The first block is based on induced rhythms, the second and the third, on evoked activity. The main part of the first block is presented by the network, which is functioning just before and after word presentation. This network is predominantly located in frontal cortical zones and consists of 38 Hz connections. The topography of this network is close to active areas revealed in PET and ERP studies, but connectivity patterns appear earlier than the activation begins. The network connects right and left cortical areas, which relate to implicit and explicit memory correspondingly (Buckner et al., 1995; Snyder et al., 1995; Badgaiyan and Posner,
This network also involves Broca area (electrodes 12 and 13). The connections bind not only frontal, but also central region (electrodes 15, 16, 47, 50 and others). This region is responsible for movement control. The generation task in its essence demands the search the action words, whose cortical representation is associated with central cortical zone (Pulvermüller, 1999; Pulvermüller et al., 1996). The next connection system inside this block includes several connections converging to right frontal area and some long diagonal connections.

As it was noted, both these networks are based on induced rhythms, i.e. oscillations, which are not time locked with stimulus delivery. Their earlier appearance leads to conclusion that they predominantly reflect the state of expectancy for immediate search for action word, associated with noun being presented. In this context, it is of interest to remind the Livanov (1972, 1986) thought that the synchronization in brain electrical rhythms signals actually not the fact of information transfer itself, but the state of readiness for this transfer. To clear up his idea Livanov used the following comparison, EEG synchronization can reveal the railway, but not the train, which is moving on it.

If the first connection block is mostly preprogrammed, two following blocks are evoked, i.e. triggered with the stimulus. The second block is formed with one network consisting of a bundle of connections binding both right and left frontal areas with left temporal–parietal zone. This information transfer is also in a rather good agreement with PET and high density ERP data, though in these studies the authors proposed that information is sent to posterior cortical areas only from the left, but not the right frontal cortex. The location of temporal–parietal area involved in this network is a bit more lateral than that revealed by ERP and is closer to that one found in PET studies. The time interval of this network functioning also precedes the activation of this zone on approximately 150–200 ms. This information transfer results in the involvement of the Wernicke’s area in word processing. This area is important for more complicated word-processing including the phrase construction (Posner and Pavese, 1998; Vorobyev, 1998). The use-generation task presents indeed a model of such simple syntactic construction. This process is probably the key act in the search for word association. It is of interest that it is executed using 22 Hz beta rhythm, which according to Whittington et al. (1997) may reflect some memory mechanisms.

The third, late block consists of two networks based on gamma oscillations. The first one is rather local and includes short connections in right frontal zone. The second network consists of long transversal connections between right and left temporal zones. This network corresponds with the activation of these areas revealed in high-density ERP study. Abdullaev and Posner (1998) conclude that this activation may reflect the involvement of insular zones responsible for planning the articulatory movements (Dronkers, 1996).

The networks in reading aloud task consist of numerous connections — their total number is much higher than in use-generation task. This fact is rather unexpected, as the reading is indeed a first step of use-generation, and it is logically to suppose, that the simpler task should involve more primitive networks. In fact, in study by Harmony et al. (1996) a more difficult task was characterized with higher connectivity, than a simpler one. However, there are also opposite evidences. As early as in Livanov’s work (Livanov, 1986), it was noted that the easier task produced rather diffuse synchronization of the brain potentials, while in the more sophisticated tasks such as synchronization, was restricted only to some local cortical areas. It our study (Ivanitsky and Ilyuchenok, 1992) it was also found that verbal task performance (anagrams solving was used) diminished the number of connections in comparison with resting state, simple and symmetrical patterns of numerous connections in rest were replaced with several ‘salient’ connections, critical for successful anagram solution.

Thus, symmetrical pattern of multiple connections in reading may reflect the diffuse, widespread synchronization of cortical rhythms, which could indicate not to the active information transfer, but the state of expectancy for active actions. In fact, rather automated reading skill...
does not demand many subjects efforts. As the method used in this study reveals not only active, but also latent connections, one may suppose that predominantly these potential connections form the massive networks, characteristic for reading aloud task. It is of interest, that numerous connections are typical not for AWC, which are more restricted, but for WCA networks, based on induced ‘endogenous’ rhythms. One of these WCA networks (that based on 21 Hz) appears before the stimulus. The proposal on the potential nature of most connections in reading corresponds to the results of PET and ERP studies, in which no additional activation in reading, in comparison with use-generation task, was revealed. The only exception was the late (800–1100 ms) activation of insular–Sylvian cortex, what was higher in reading, than in use-generation.

Still, if even the most connections, revealed in reading, are potential, their general configuration shows the cortical areas and their interactions involved in reading. This configuration differs significantly from that in generation. The areas, characteristic for reading, include occipital, parietal, temporal and central zones and only several points in frontal cortex. In contrast, the cortical connections in creative use-generation task involve predominantly the frontal areas, especially during two first stages.

The problem is, however, why networks, characteristic for reading, are absent in use-generation task. One may suppose that, when more difficult task is presented to the subject, these rather massive networks based on diffuse synchronization don’t actually disappear, but become as to be shadowed by the other networks. The latter consists of several specialized connections crucial for this more difficult task solving. The intimate mechanism of this shadowing could be as follows. More complicated task, such as use-generation, re-allocates the brain activity to the areas involved in more difficult operations and relatively attenuates the activation of the other cortical zones making the signs of their interaction below of resolution threshold of the method. The drop of the CC values for networks characteristic for reading, while performance of use-generation task, confirms this proposal.

It is of special interest that three of five networks in reading task have the same frequencies as the networks functioning in use-generation. These frequencies are 22, 29 and 41 Hz. One may conclude that these frequencies, probably, play a particular role in brain mechanisms involved in word processing. This proposal coincides in part with data by Lutzenberger et al. (1994), who reported approximately the increase of 30-Hz oscillations in verbal task performance, particularly while reading meaningful words, in comparison to pseudowords.

The analysis of the correlation coefficients in use-generation and reading aloud tasks supply the experimenter with additional data for understanding how information transfer in the brain is executed. The connection networks described above have been revealed, basing on the fact, that the CCs in this given task is higher than in another compared task. The connection is usually found when CC value reaches its maximum at the define point of the time scale and when the CC difference becomes to be statistically significant. It is of interest, however, that the curve of the coefficients in a compared task is not flat. As a rule, at critical points of information transfer the increase of the coefficient value in one task is accompanied with the concordant decrease of the CCs in another task. There are two possible mechanisms of this event: one is more probable for networks executing reading task; and the other, for networks functioning in use-generation.

The first mechanism was already described earlier. The decrease of CCs in networks typical for reading, while executing of use generation can explain the fact why the multiple connections, characteristic for reading, disappear in performance of use-generation task. This decrease of CCs presumably is the result of the re-allocation of the attention to more difficult operations. As a sequence, processes, which underlie easier task, become less prominent.

But while reading the compared values of coefficients in use-generation never cross the zero line. The opposite situation is in AWC networks, typical for use-generation, at the maximum point of coefficient value in generation the coefficient value between the same electrodes in reading
becomes negative. It means that when the wavelet power increases in one of two compared cortical sites, it diminishes in another site. We propose that this decrease of wavelet power can perhaps evidence to the active process of the inhibition, which prevents the information transfer to this area. This prolonged inhibition is evident of other nature, than that used in short term communications between neuronal groups, which is controlled only by phase relationship. If this proposal is correct, the following explanation of the negative shift of the correlation coefficient values can be suggested. The reading of the single words is rather an artificial situation, specially applied for research purposes. Usually the noun is accompanied with verb and only this pair has its own sense, express a definite thought. Therefore, while performance of the reading-aloud task the usual circuitry of cortical connections is interrupted due to switching on the inhibitory mechanisms.

Let us make a more general conclusion. Almost all our tasks we use to study the brain base of mental functions are more or less artificial. These limitations are inevitable, because they permit us to decompose the complex functions to its elements and enable to understand the nature of brain processing. But in fact, the general scheme of brain communications is much more sophisticated, than that we can now reconstruct using our methods. There are many connections inside the cerebral cortex, both inborn and acquired during ontogenesis due to learning process. The execution of any particular function uses only necessary connection, selecting them of the whole communication system. This selection is based both on the principle of coinciding frequency patterns and due to inhibition of all excessive connections.

Thus, the carried out study concentrated on spectral EEG rearrangements can contribute to further understanding of brain mechanism of thought evidencing not only ‘where’ but also ‘how’ information is processed inside the cortex.

Acknowledgements

We are grateful to Professor M.I. Posner and Dr Y. Abdullaev for supplying us with ERP recordings in use-generation and reading aloud tasks, for kind co-operation while carrying out this study and for their valuable comments to the text of this paper. This work was supported by grants from James S. McDonnell Foundation and Pew Memorial Trust No. 97-38 ESSI, from Russian Foundation of Basic Researches No. 99-04-48229 and from Russian Scientific Foundation for Humanities No. 99-06-00059a.

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