Reflection of the Pattern of Cortical Activation in the Phase Structure of the Human EEG

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A total of 22 healthy subjects in the EEG laboratory and 62 patients in the clinical functional diagnostic unit were studied. Spontaneous EEG recordings were made using the 10–20 scheme relative to combined ear electrodes in the state of rest with the eyes closed and open and during various functional loads. Traces were analyzed by computer animation of the EEG phase structure. The main concept of the method for extracting phase structure was based on not using a single reference lead. Time shifts were measured only between neighboring electrodes, with the result that the oscillations being compared were highly coherent. Time discordance was assessed in terms of the shift in the peak of the cross-correlation function. The results showed that from the point of view of phase structure, the differences between the high- and low-frequency EEG rhythms were purely quantitative. Qualitatively, the properties of the rhythms were identical and were reduced to slow (in the seconds range) oscillations of phase shifts. Low-frequency activity was characterized by large (in absolute terms, msec) phase shifts from electrode to electrode as compared with high-frequency activity. The phase shifts of potentials formed a structure which was overall very similar in different subjects and was reproduced in different leads. The initial appearance of EEG waves was statistically linked with the main sensory projections – the visual (occipital areas), auditory (temporal areas), and somatic (parietal areas), with addition of the frontal areas. Rearrangement of phase leadership in favor of the occipital pole at the expense of both temporal areas was observed on opening the eyes. This appears to depend on the level of sensory influx to this cortical area from the thalamus. It is suggested that the direction of the phase gradient reflects a gradient of cortical current density parallel to the surface. This can be used to locate compact sources lying close to the surface.

KEY WORDS: EEG phase structure, moving wave, cortical activation, individual variation, current density.

Data on EEG phase relationships in different areas of the cortex are very contradictory and do not point to any single interpretation. Different opinions exist in relation to the mechanisms forming the gradient of the phases of oscillations from electrode to electrode. According to one point of view, propagation of an electric potential across the surface of the cortex reflects the physiological interaction of neurons (physiological coordination) [31, 41, 42]. Another view holds that there is no true physiological displacement across the cortex and that the apparent movement is due to electrical interference between oscillations in the good conducting conditions (physical induction) [45]. Both concepts have satisfactory experimental foundations and exist in many variations. Mention can be made of information scanning in cortical transmission [21, 26, 27, 43], the single moving wave hypothesis, which emphasizes the link with the element-synchronizing process [23], and the thalamic pacemaker concept [12, 25]. Another group includes numerous models based on interference from several compact generators [36, 39, 45] and the standing waves model [35, 52]. The equivalent current dipole method has met with success [5, 8, 46, 51].

Each particular case would seem to be associated with the operation of one mechanism or another [23]. Important

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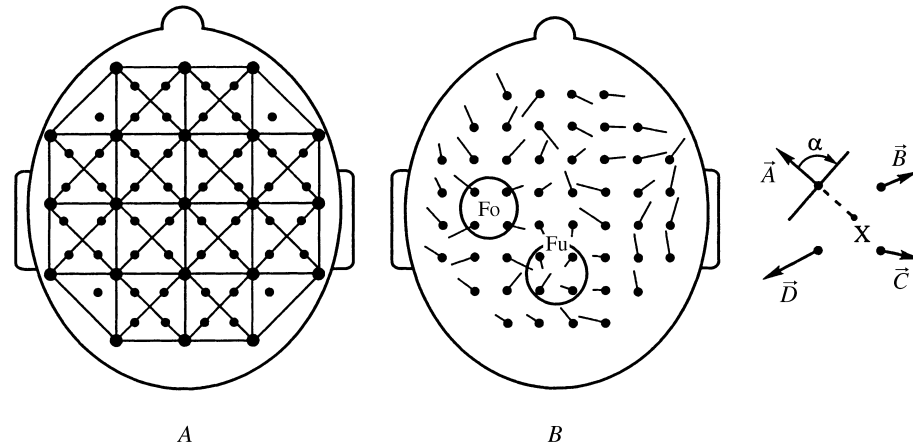
Fig. 1. Diagram showing measurements of EEG phase structure. *A*) Division of the electric field into triangular segments, each of which was used for construction of a potential wave movement vector. Large black dots show electrodes (10–20 system); small dots show points neuron from which vectors were plotted; *B*) example of a vector structure with a "focus" (Fo) and a "funnel" (Fu); *C*) calculation of phase leadership for point *X*, surrounded by four vectors (see text for explanation).

information about this can be obtained from the rate of movement of the potential wave (or the rate of movement of isoelectric lines). According to simulation studies and direct measurements, this rate can be sharply different for different examples of the mechanisms listed above [27, 28, 32, 34, 38, 48, 52].

Most studies to date have been based on the paradigm of a single reference lead, i.e., all oscillations are compared with any one point on the surface of the head. This strongly restricts the range of investigations, as it requires oscillations to have a high level of spatial coherence. In fact, this approach can provide adequate assessments of phase structure only of the hypersynchronous alpha rhythm, which is present in a small number of people or for a minor proportion of time. Generalized paroxysms of different causes can also be assessed. In some cases, distant points show small numbers of oscillations, though it is meaningless to compare these in terms of phase. This problem can be avoided by dividing the study field into local areas and, for all cases, to compare only the neighboring oscillations. These are guaranteed to have high coherence and, therefore, to be comparable. However, the evaluable phase shifts in this situation are known to be small, such that high sampling frequencies are needed for them to be measured. The instrumentation must also be highly sensitive [2, 3].

METHODS

Studies were performed on 22 healthy volunteers in the EEG laboratory, along with 62 patients in the clinical functional diagnostic unit after referral by neurologists with medical indications for EEG studies. Spontaneous EEG recordings were made in all subjects using the standard 10–20 scheme by a monopolar method relative to combined ear electrodes. In the clinic, 1-min EEG recordings were made from 21 electrodes (Fig. 1, *A*) using a Mitsar electroencephalograph (St. Petersburg, Russia) at rest with the eyes closed and open; traces were recorded on computer with a sampling frequency of 250 Hz. EEG traces were recorded over the frequency band 1–70 Hz. The noise level in this band was no greater than 2 μV. The time constant was 0.3 sec.

Patients generally had histories of headache, sleeplessness, vertigo, tiredness, irritability, and deterioration of memory and attention. Many had histories of previous cerebral concussion and head trauma, the sequelae of neurological infection, and strokes, as well as hypertension, diabetes, and other diseases. The group consisted of 18 men and 44 women; patients were aged 18–70 years.

In laboratory studies of healthy volunteers, 15 electrodes were located in a rectangular pattern of 3×5 points in a truncated version of the 10–20 scheme, i.e., without the temporal circuits. The sampling frequency was 500 Hz per channel. Healthy subjects were aged 18–30 years and there were equal numbers of males and females. Recordings were made both at rest with the eyes closed and open and during application of various functional loads: visual following, listening to music, and more. These included immersion of the face into cold water with breath-holding [6].

Apart from the standard medical EEG reports (for doctors), all traces were analyzed by computer animation of phase structure, as described in detail elsewhere [2, 3]. The main concept of this method of extracting EEG phase structure consisted of elimination of the use of a single reference lead. Time shifts were only measured berween neighboring electrodes, with the result that the oscillations being compared were always highly coherent. Time discor-

dance was assessed not in terms of the delay of concordant phases but in terms of the displacement of cross-correlation function peaks (in units of time). This measure is applicable to oscillations of any frequency composition.

The electrode field was divided into triangular segments, as shown in Fig. 1, *A*. In each triangle, time displacements relative to the right angle were measured at the other two angles. These orthogonal displacements were used to construct a vector identifying the source from which the potential wave front moved to the point concerned (the vector was perpendicular to the wave front). The vector originated from a point in the center of the triangle; its length was proportional to the rate of movement of the wave. The resulting system of ordered vectors provided a description of the EEG phase structure (Fig. 1, *B*).

Vector structures were calculated for sequential analysis epochs of 0.1 sec (essentially a single alpha wave) and served as frames for computer animation, which could be viewed in slow motion, fast motion, or live speed. Data were smoothed over time, i.e., animations were constructed using a sliding mean of data from several frames (see below for more detail).

In earlier studies, electrodes were distributed in a 4×4 square in the parietal-occipital area [2, 3]. As oscillations in neighboring leads usually showed only a very small time shift, a high sampling frequency was needed – the closer the electrodes, the greater the sampling frequency required. At an interelectrode distance of 2–3 cm, recording of the alpha rhythm required a sampling frequency of at least 500 Hz per channel; time resolution for higher frequencies was obtained by spline interpolation, i.e., calculation of additional data points between those actually measured. This method allows for unlimited increases in the precision of the description of phases, though in practice 2000 Hz was adequate.

The interelectrode distance in the present study was increased to about 5 cm (on the 10–20 system). This decreased the required sampling frequency to 250 Hz – this frequency was used for investigating patients (500 Hz was used for healthy subjects). Spline interpolation was used during processing of data from all subjects (patients and healthy volunteers) to increase this to 1000 Hz per channel.

All frame-by-frame phase structures were stored as text files, each frame corresponding to a row including all calculated interelectrode shifts (in msec). These files were subjected to statistical analysis to verify the statistical significance of the findings. Preliminary studies identified the periodic appearance of phase structures with epicenters or foci in all subjects; these had very interesting properties [3]. Vectors from several points on the head were sometimes directed in different directions, i.e., the potential wave propagated concentrically from a site. Structures which we termed potential discharge currents or "funnels" were also found, where several neighboring vectors were all directed towards a single point (Fig. 1, *B*). The incidence of these structures was

assessed quantitatively using the phase leadership coefficient (PLC). This was calculated for each point of the head surrounded by four vectors (Fig. 1, *C*). Each of the vectors $\vec{A}$, $\vec{B}$, $\vec{C}$, $\vec{D}$ contributes to the coefficient depending on its direction expressed as the sine of the angle between the vector itself and the sideways to the right direction. If vector $\vec{A}$ was directed away from the point being assessed, *X*, then the sine of angle *b* is (+1). If vector $\vec{A}$ is directed towards point *X*, then the sine of *b* is (–1). Thus, PLC for point *X* can have values from (+4), when point *X* gives rise to the focus, to (–4), when point *X* forms a "funnel."

Values were calculated for the coefficient for each analysis epoch, which was 0.1 sec (i.e., each frame), for 57 points on the surface of the head. A modified coefficient was used for points at the periphery of the electrode field, taking account of the "incomplete set" of vectors (there were vectors on only one side of the point of interest). Spatial phase leadership patterns were identified using a specially written animation program allowing maps to be overlaid on a three-dimensional model of the cortical hemispheres. Similar three-dimensional animation is used in computer games. Foci with high leadership coefficients were identified on animations in red, "funnels" in blue, and intermediate values in green; transitions between colors were smooth. The brain model could be rotated to allow examination from any angle, with any desired smoothing of the data in time and any replay speed (rate of frame changes).

Additional experiments for refining and monitoring the experiments were performed depending on the results of statistical analysis of the EEG data.

RESULTS

Rate of movement of potential waves. Phase shifts between neighboring electrodes, measured as described above, were not constant during the recording period and showed wave-like oscillations from epoch to epoch, with a period of 1–2 sec. Typical examples of these dynamics over a period of 4 sec are shown in Table 1. The purely numerical data presented in Table 1 correspond to the EEG traces shown in Fig. 2. The EEG trace of the theta paroxysm shown in Fig. 2, *1* was recorded in a clinical patient using the complete 10–20 system, i.e., 21 electrodes (only 15 are shown). The traces in Fig. 2, *2*, *3*, *4* were made on a healthy volunteer.

The data presented in Table 1 show that the wave-like dynamics of interelectrode phase shifts was characteristic for different types of EEG rhythms, though with different absolute values (in time units). The greatest discordance between neighboring EEG traces were seen at the peaks of 2-sec oscillations in a generalized theta paroxysm at 5 Hz (see Table 1; Fig. 2, *1*). Taking cognizance of the 5-cm distance between the electrodes, the rate of movement of the

TABLE 1. Sequential Measurements (msec) of Discordance of Oscillations in Neighboring Electrodes Located at Distances of 5 cm

ID No. of 0.1-sec (frame) analysis epoch	Generalized theta paroxysm		Occipital alpha rhythm		Polyrhythmic oscillations (IPSA, FAA)		Recovery after immersion test	
	in the longitudinal direction	in the transverse direction	in the longitudinal direction	in the transverse direction	in the longitudinal direction	in the transverse direction	in the longitudinal direction	in the transverse direction
1	−2	31	12	−8	0	0	0	0
2	−7	20	13	−12	0	0	0	0
3	−27	4	22	−17	0	−1	0	0
4	−24	9	16	−14	0	−2	0	0
5	−13	16	16	−8	−1	−3	0	0
6	−19	18	0	1	0	0	0	0
7	−31	21	7	−4	0	−1	0	1
8	−30	12	5	−5	0	−4	0	1
9	−28	14	3	−4	0	−5	0	0
10	−31	22	1	0	0	−3	0	0
11	−31	19	−1	4	0	0	0	0
12	−31	31	−2	7	0	0	0	1
13	−31	31	−5	11	0	−1	0	0
14	−31	27	−7	11	0	−2	0	1
15	−31	21	0	4	−1	−4	0	1
16	−31	27	11	0	−1	−3	0	1
17	−31	31	14	−3	−1	−5	0	0
18	−21	6	10	−5	−1	−7	0	0
19	31	1	6	−9	−1	−2	0	−1
20	31	0	6	−8	−1	−1	0	−11
21	10	1	6	−6	0	−1	0	0
22	−20	4	6	−5	1	−2	0	1
23	−31	8	5	−2	1	−2	−1	5
24	31	17	3	−2	0	0	−2	5
25	31	9	0	0	0	4	−1	4
26	31	25	−2	1	−1	3	0	6
27	11	15	−4	−1	−1	4	0	9
28	31	17	−4	−1	−3	1	−1	9
29	31	19	−3	−3	−3	0	0	8
30	31	28	3	−3	1	−0	0	8
31	31	27	4	−2	0	−1	0	11
32	31	23	3	−1	0	0	0	12
33	−31	24	1	−1	−2	0	0	13
34	−31	−3	2	−5	−2	1	0	11
35	−31	3	1	−6	0	2	−1	11
36	−31	17	3	−11	1	2	−2	2
37	−31	8	5	−3	0	2	0	1
38	−31	27	9	−2	0	1	−12	0
39	31	23	10	−3	−1	0	−12	1
40	31	11	9	−2	−1	0	−12	0
Mean of absolute values	27	16.8	6	4.9	0.6	1.8	1.1	3.4

Notes. Measurements for one triangular segment are given, i.e., in adjacent pairs of electrodes. Each pair of numbers identifies one local vector in the composition of vector structures shown in Fig. 2, *B*.
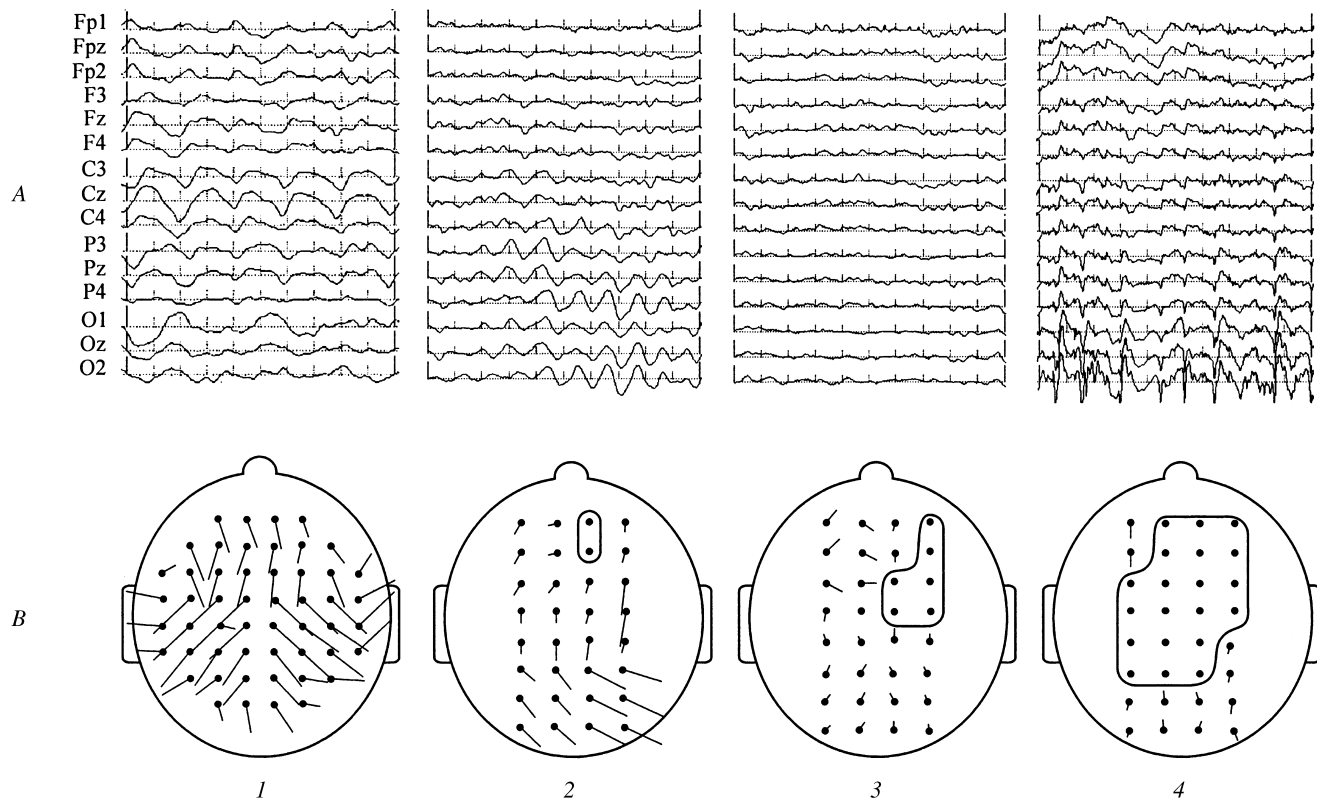
Fig. 2. Examples of 1-sec initial EEG trace segments (*A*) and their corresponding phase structures (*B*). *1*) A theta paroxysm; *2*) resting alpha rhythm (eyes closed); *3*) polyrhythmic EEG (at rest, eyes open); *4*) EEG on excitation. The magnitudes of local phase shifts are indicated by vector lengths. Vector directions show the direction of movement of wave fronts. Areas of completely synphasic oscillations are enclosed in lines.

wave at these times was less than 2 m/sec. The series of several identical measurements at 31 msec occurred because values went beyond the range of the apparatus, so the actual speed was thus about 1 m/sec.

In healthy subjects with clear alpha rhythms in the occipital areas, large phase shifts were generally recorded in these areas, though they were smaller than the theta rhythm; shifts were even smaller in the anterior areas (see Table 1). The vectors were longer where the alpha rhythm was more marked (Fig. 2, *2*). This was supported statistically by spectral analysis. The local phase shift in this area of the head, averaged for the whole analysis epoch (seconds, tens of seconds), correlated closely with the spectral power of the alpha rhythm in this area during the same epoch. In the case presented in Fig. 2, *2*, the rank correlation coefficient between these measures for 15 recording points was 0.80 ($p = 0.003$). This was always seen in the state of resting with the eyes closed except in those cases in which the pattern was distorted by antiphase frontal and occipital oscillations (see below).

The frontal areas of this subject showed irregular polymorphic slow activity (IPSA) with an admixture of fast asynchronous activity (FAA), which for convenience we will term "polyrhythmic" activity. The same activity was seen when alpha activity changed, as well as in the parietal-occipital areas on opening the eyes – this case was quite typical. All areas showing polyrhythmic activity, like those with theta and alpha rhythms, showed ordered vector patterns (Fig. 2, *2*, *3*). In other words, the phase structure was also ordered in the presence of polyrhythmic activity, i.e., there were consistent gradients of phase oscillations from electrode to electrode.

The only difference from the slow rhythms was that the vectors in polyrhythmic activity were shorter, i.e., phase shifts were overall smaller (in msec) and the speed of potential wave movement was correspondingly faster. This is supported by the data shown in Table 1. Polyrhythmic activity also showed slow (in the seconds range) waves of phase shifts, though even at their peaks their absolute values were no greater than 5 msec. Shifts of 1 or 2 msec were most commonly seen, i.e., at the limit of the sensitivity of the apparatus. A phase shift of 1 msec corresponds to a rate of movement of isopotential lines of 50 m/sec.

Virtually all patients showed decreases in interelectrode shifts in the occipital areas on opening the eyes ($p < 0.001$ on average for the group); spontaneous blockade of the
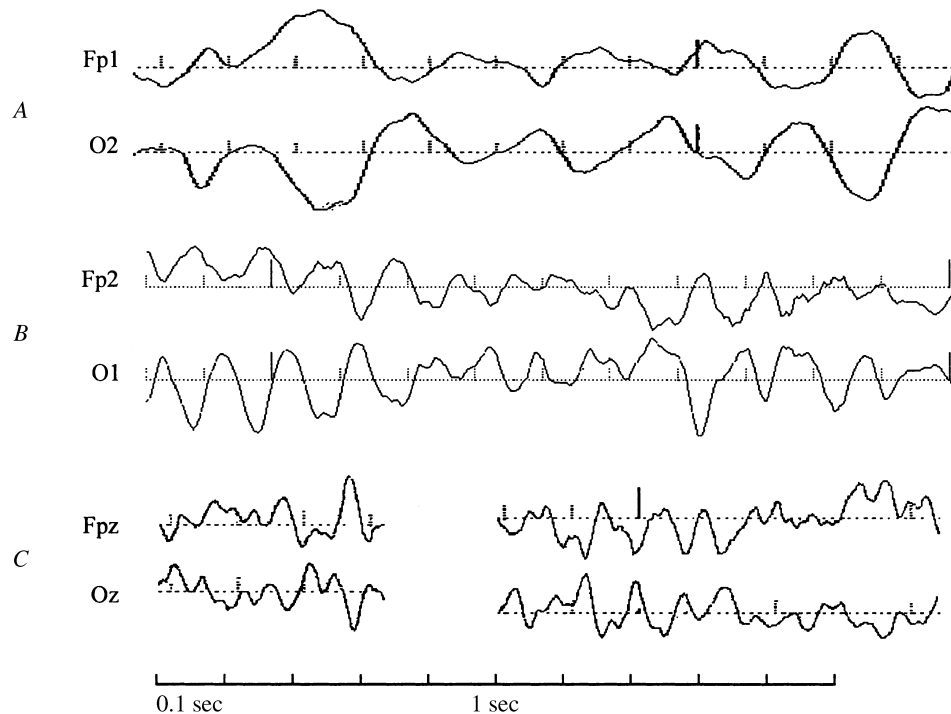
Fig. 3. Antiphase relationships of oscillations in the frontal and occipital areas. *A*) For the theta rhythm; *B*) for the alpha rhythm; *C*) for fast rhythms and polyrhythmia.

alpha rhythm was sometimes seen on closing the eyes. The same patterns were clearly seen in the preceding study, performed on healthy subjects with occipital electrodes [3].

In some functional loadings, the ordered phase structure disappeared and was replaced by completely synphasic oscillations over space or an "infinite" speed of wave movement (for the level of sensitivity of the apparatus). In these conditions, the EEG showed polyrhythmic fast oscillations characteristic of strong activation (Fig. 2, *4*). For example, this was seen in healthy subjects on immersing the face in cold water with breath-holding (an analog of washing in the morning). The electrodes for these recordings were located both in the 10–20 scheme and as dense 4 × 4 blocks in the parietal-occipital area. Similar results were obtained with both electrode distributions. This pattern of generalized activation often occurred before immersion of the face into water, i.e., during preparation for the action. Oscillations at neighboring points were virtually identical, i.e., there was complete spatial synchronicity, which is known not to occur at rest (Fig. 2, *4*).

The process of restoration of the normal rhythm after tests were ended was informative. Continuous EEG activation with completely synphasic oscillations persisted for some period of time (seconds). The periodic "slow" movements of EEG waves then reappeared, i.e., the non-random structures of phase shifts reappeared in various sites every 1–2 sec and were again replaced by synphasic oscillations.

Over an interval of 10–30 sec, completely synphasic oscillations gradually shortened while "slow" oscillations lengthened and became more marked, thus restoring the initial wave-like rhythms of speed and trajectory.

Areas of completely synphasic oscillations could be seen in different states (grouped together in Fig. 2, *B*, *2*, *3*, *4*), though they were more characteristic and occupied a greater area in cases of stronger activation on the EEG of the active state. They could sometimes cover almost the whole cortex (Fig. 2, *4*).

Thus, differences between high-frequency and low-frequency EEG rhythms, from the point of view of spatial phase gradients, were purely quantitative. Qualitatively, the properties of rhythms were identical and reduced to wave-like oscillations in the phase shifts under observation. It should also be noted that the absolute values of phase shifts far from always corresponded to the amplitude of oscillations at the site concerned (though this impression can be gained from the examples presented).

Antiphasic nature of frontal and occipital oscillations. An effect linked with the known antiphase EEG oscillations in the frontal and occipital areas was superimposed on these characteristics. Antiphase oscillations were seen for activity at all frequencies. This was clearer for theta and alpha waves, while for short and small waves the effect was less marked but still undoubtedly present (Fig. 3). The commonest finding was a frontal alpha rhythm in
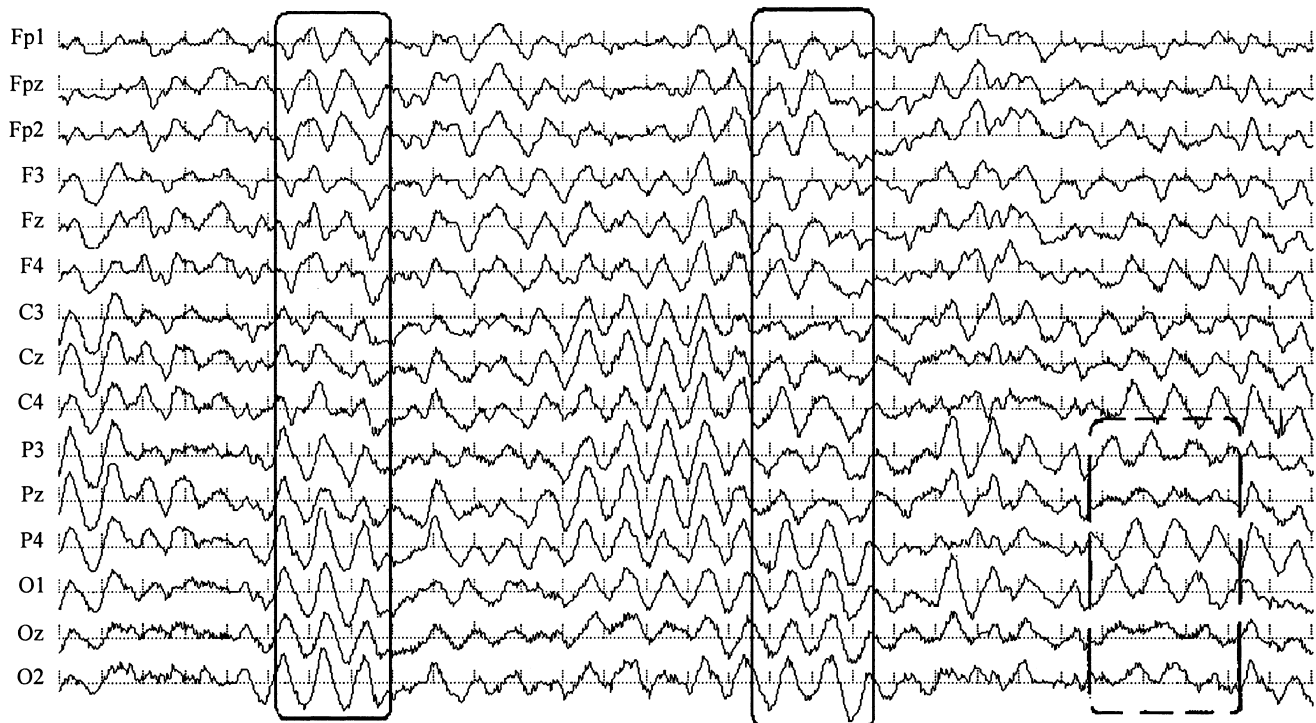
Fig. 4. Hypersynchronous alpha rhythm with areas of antiphase between the frontal and occipital areas (enclosed in continuous lines) and antiphase between the left and right areas (enclosed in dotted lines).

antiphase to the occipital alpha rhythm. The term "standing wave" is used to describe this phenomenon in the literature [32, 34, 35, 52]. It has also been noted repeatedly that the tendency for oscillations in frontal and occipital activity to be in antiphase is independent of frequency and brain size (for example, this effect is seen in rabbits) [1, 20, 23, 33, 40].

The examples presented in Fig. 3 leave no doubt that the situation is not one of oscillations shifted by one half-period but one of synphasic inverted oscillations. This is because there is coincidence not only of phase, but also amplitude and the fine details of wave shapes. It is unlikely that this pattern could arise from physiological coordination via the superior longitudinal bundle [23]. It is more likely that the effect results from some property of the brain such as volume conduction.

In our studies, this effect was clearly and constantly apparent in virtually all patients; it was much less characteristic of healthy volunteers. The antiphase nature of oscillations was clearly seen in 10% of healthy subjects, but was present in most on a periodic basis. Antiphasicity in healthy subjects was mostly present in cryptic form, as slightly negative cross-correlation coefficients between the anterior and posterior leads, of the order of (–0.10)–(–0.20).

A healthy subject with a clearly evident hypersynchronous alpha rhythm over the whole surface was selected for illustration. Very different spatial amplitude and phase

gradients were found (Fig. 4). At those moments at which the antiphase nature of oscillations was most apparent (enclosed in continuous lines), the vertex area, because of phase inversion, showed a decreased amplitude and an unstable wave shape, i.e., sharp changes in the forms of oscillations from point to point. In our method of assessing phase shifts, this led to an abundance of sharply increased phase shift values in this area because of the non-coherence of the components of neighboring oscillations. It is interesting that analogous antiphase relationships between symmetrical regions on the left and right sides were sometimes seen (enclosed in dotted lines in Fig. 4). In this case, the decrease in amplitude and the instability of the waveform occurred at the central sagittal line, which was apparent as an "axis of symmetry."

Similar data on the frontal alpha rhythm, coherent with the occipital, are present in the literature. These studies also noted the presence of a sharp delimiting zone at the site of phase inversion, where oscillations were non-coherent with the initial oscillations, i.e., those in the frontal and occipital areas. This zone showed a step in the phase; discordance between neighboring leads in the two halves was small [23, 33, 37, 49].

This raises the question of why the antiphasicity effect is more marked in patients. It is likely that this is in some way linked with the positioning of the indifferent electrode
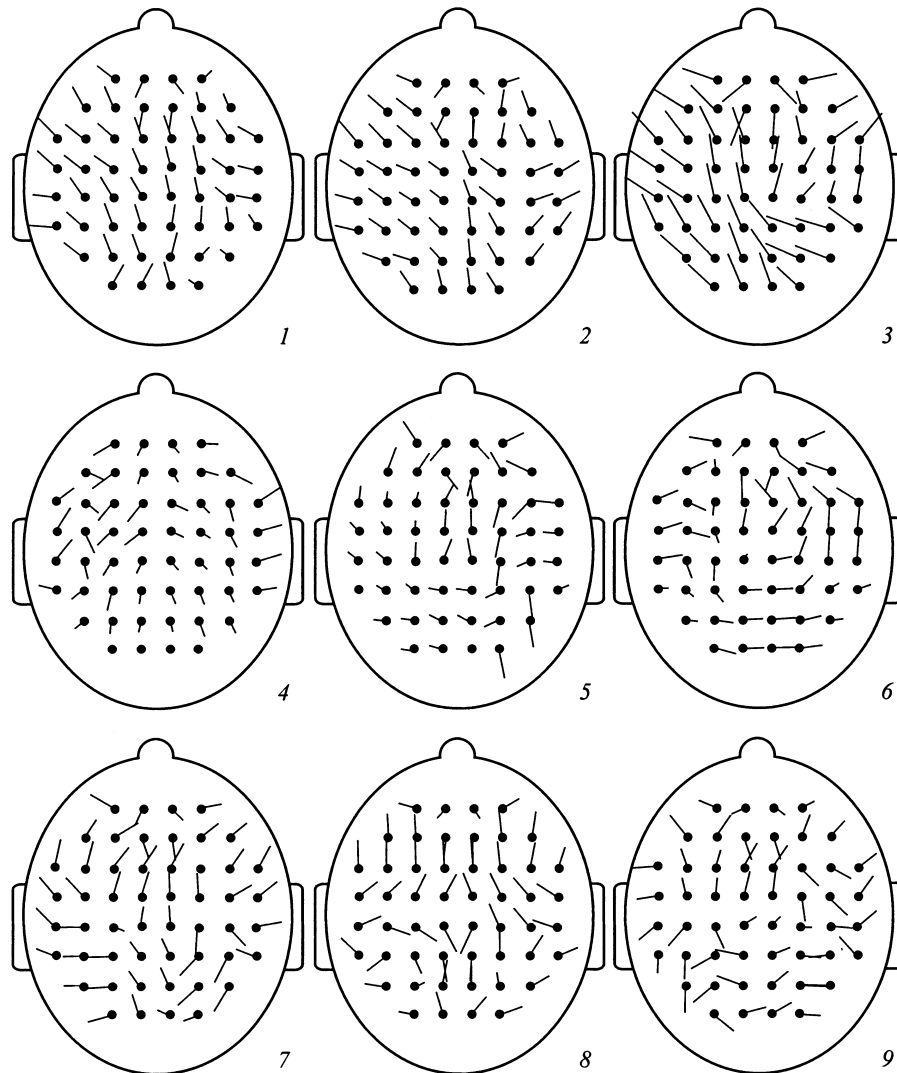
Fig. 5. Examples of individual vector (phase) structures from different subjects obtained by accumulation statistics on interelectrode phase shifts over prolonged periods (1 min).

on the ear lobes, i.e., essentially midway between the frontal and occipital areas. The indifferent electrode was located identically in patients and healthy subjects, though the input resistances of the amplifiers were different (150 versus 90 MΩ). There is almost no doubt that the clear differences between patients and healthy volunteers in this case arise from the characteristics of the recording instruments. An increase in the input resistance leads to redistribution of currents in the overall electrode system–amplifier system complex (the actual set-ups are not shown here for economy of space). There is no support for the notion that the brains of patients were more "electrically transparent" than those of healthy subjects.

It is known that the frontal alpha rhythm is not seen in conditions of bipolar recording [7, 23, 47]. Frontal oscilla-

tions in antiphase to occipital oscillations are strongly dependent on both the recording set-up and the parameters of the instruments. Is there any doubt that they are being distorted by the instrumentation? However, the antiphasicity described here does not appear to be a technical artifact, but, rather, a real phenomenon. This is evidenced by the high degree of "transparency" of the brain for some electrical processes and is supported by the concept of standing waves.

Models of CNS functional states in humans. Visual analysis of initial EEG traces from patients allowed them to be divided into groups in accord with the classification of Svyatogor [18].

1. The presumptively normal group. The EEG of 18 subjects showed a clear fusiform alpha rhythm. Rhythmic photostimulation showed quite clear assimilation.

2. The thalamic group. The EEG in 19 subjects was characterized by a dominant alpha rhythm, distorted by grouped delta and theta waves or bursts of regular theta rhythm at a frequency multiple of the alpha rhythm. Rhythmic photostimulation produced clear assimilation. These features were characteristic for lesions of the cortico-subcortical interactions at the level of the thalamic formations.

3. The stem group. The EEG in 18 subjects was characterized by low-amplitude polymorphic slow activity (IPSA) with admixtures of frequent asynchronous activity (FAA), i.e., polyrhythmic oscillations, with the highest level of assimilation of rhythms on photostimulation. This symptom complex indicates an increased level of ascending activatory influences due to lesions at brainstem level.

4. The cortex group. The EEG of 7 subjects showed a hypersynchronous unmodulated alpha rhythm and complete lack of responsiveness to photostimulation. This EEG pattern is evidence of decreased cerebral cortical tone.

The nervous system abnormalities diagnosed here were not associated with destructive changes in brain tissue but with impairment of the general functional state of the CNS. These EEG types were considered further as models of four different functional states, reflecting both normal cortical-subcortical interactions (the normal group) and predominant levels of impairment of regulatory mechanisms (the thalamus, stem, and cortex groups).

Trajectories of moving potential waves. The directions of movement of potential waves were very diverse and variable even in particular individuals – both healthy subjects and patients. Some subjects showed a predominant direction of movement, a direction in which most vectors were most frequently aligned. Averaging of analysis epochs for all EEG traces allowed identification of the trajectories of moving waves occupying the greater proportion of the observation time, even in subjects with poorly marked predominant directions.

Patients most commonly showed a direction from the occipital zones to the frontal, with some deviation in the diagonal directions; vectors were mainly directed from the right posterior zones to the left anterior zones (Fig. 5, *1*, *2*, *3*). This applied to 28 of the 62 patients. This diagonal asymmetry was completely consistent with the results obtained in previous studies using parietal-occipital electrodes in healthy subjects [2] and with published data [4, 16, 17]. Healthy subjects showed identical incidences of movement in both directions along this diagonal – forwards and backwards [2, 23]. We note that in using the concept of a diagonal trajectory, we do not indicate that absolutely all trajectories were aligned in a single direction. A quite large proportion of vectors can be aligned in different directions, though the pattern overall can demonstrate the diagonal nature. The same applies to other types of trajectory.

Other dominant directions were found much less frequently. In particular, predominant propagation of waves from the frontal area to the occipital occurred in two

patients, and clockwise and anticlockwise rotation was seen in three and two patients respectively (Fig. 5, *4*, *5*, *6*). A characteristic trajectory in some subjects was seen only with the eyes open, in others only with the eyes closed, and in others in both situations. Phase patterns very commonly showed a combination of different types of trajectory. Finally, there was a significant number of subjects in whom no dominant direction could be identified. Their trajectories were so intricate that formal verbal descriptions could not be applied. The potential field was not a single entity, but was divided into separate (sometimes numerous) regions, within which the directions of potential movement were independent of each other. The vector structures were further complicated by the presence of foci and "funnels," where potential waves were distributed concentrically around a local point (Fig. 5, *7*, *8*, *9*; see also Methods). Such complex structures arose periodically in subjects who at other times showed simpler structures with a dominant direction.

Statistical analysis. Different areas of the cortex were compared with each other in terms of the frequency of appearance of foci and "funnels" and different groups of subjects were also compared using the phase leadership coefficient (PLC) (see Methods). We note that high values of this coefficient indicate that EEG oscillations in the area concerned arise earliest; low values identify delays in waves in the area concerned.

The very large volume of data (57 coefficients for the whole of the head surface) raised the question of how to combine them into relatively small groups. This was approached using cluster analysis for the set of 62 patients (tree clustering, Ward's method, Euclidean distances). In the state of rest with the eyes closed, this showed that the closest measures were located either symmetrically or in series in defined areas on the head surface, only some locations showing a mosaic distribution. The grouping results replaced the 57 series of coefficients with a total of five (Fig. 6, *A*). Two groups (the temporal and the central) were heterogeneous and involved, apart from these regions, a series of mosaiform coefficients. In these heterogeneous groups, we elected to average only those measures located compactly side by side, in the two temporal areas and the central area, without consideration of mosaiform parameters.

On average for all patients, the greatest phase leadership was seen in the frontal area. An occipital focus could also be identified, while the central area had a coefficient of intermediate value. The smallest values were seen in the precentral area on the margin of the frontal area, as well as in the two temporal areas.

Correlation analysis showed that a number of subjects had a positive relationship between the central and occipital areas ($p < 0.00001$) and a negative correlation ($p < 0.01$) between these areas and the prefrontal and both temporal areas. This means that if a given subject showed high coefficients in the occipital area, values in the central area would
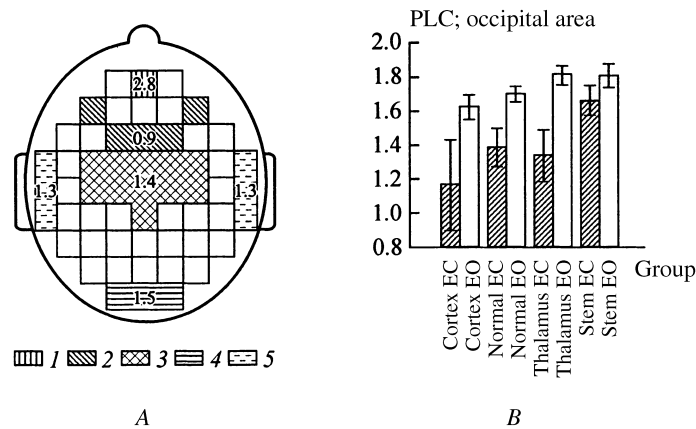
Fig. 6. Results of statistical analysis. *A*) Areas of relatively independent groups of phase leadership coefficients (PLC) identified by cluster analysis; *1*) frontal; *2*) precentral; *3*) central; *4*) occipital; *5*) temporal; *B*) dynamics of phase leadership PLC in four groups of patients with different types of EEG abnormalities at rest with closed (EC) and open (EO) eyes, using the occipital area as an example.

also be high, while values in both temporal areas would be low. These individual differences appeared to be associated with the assignment of the subject to one or another of the groups of patients. The cortex group lacked the occipital focus; the stem group, conversely, had the most marked occipital focus of all patients but no temporal foci.

Some subjects showed a sharp contrast between measures in different areas; others had a smoother distribution. In particular, the stem group was characterized by the highest level of contrast, while regional differences were least marked in the cortex group. The normal and thalamus groups occupied an intermediate position in terms of mean leadership values in different areas and in terms of contrast. They differed from each other only in the frontal area – frontal phase leadership was greater than in the thalamus group.

In the eyes open situation, the structure of values identified by cluster and correlation analysis was essentially identical to that in the eyes closed situation. This allowed both states to be compared separately by area. All cases showed identical reactions to eye opening: phase leadership decreased significantly in the frontal area, increased in the prefrontal and occipital areas, and remained unchanged in the central area. The temporal areas showed a decrease in the leadership coefficient in all groups on eye opening ($p < 0.001$ on average for all subjects, ranging from 0.01 to 0.05 for individual groups). This dynamic did not alter the overall relationships between regions or between groups of subjects. Data for the occipital focus are presented in Fig. 6, *B* for illustration.

Overall, brain potential phase shifts formed a defined structure, which was overall very similar in different patients and was reproduced in both of the states investigated. We believe that this structure is in good agreement with the anatomy of the main sensory projections – the visual (occipital), auditory (temporal), and somatic (parietal area), with addition of the frontal region. The actual values of the leadership coefficient in one region or another appear to be determined by the level of sensory input to the region of the cortex from the thalamus. This may explain the redistribution of leadership in favor of the occipital pole at the expense of both temporal areas described on opening the eyes. The sense of the parameter leads to the view that the statistical features of foci giving rise to EEG oscillations are in some way linked with the major sensory projections.

There is now evidence that the sources of rhythms, at least the alpha rhythm, are located in the area of the cortical end of the corresponding analyzer, i.e., each sensory projection to the cortex has its own local spontaneous rhythm. Spontaneous rhythms in the alpha range can be termed "sensory-specific." They are seen when the cerebral cortex perceives afferent information from underlying structures [10, 46, 50].

DISCUSSION

As already noted, the observed speed of wave propagation is an important argument in favor of one or another mechanism. There are both theoretical and experimental numerical assessments of the speed of potential waves for the case of physiological coordination, i.e., interactions between cells. For circuits consisting of close-lying short-axon connections, the speed of alpha waves in the neocortex should be 4–20 m/sec, while the speed for long corticocortical connections should be 6–9 m/sec [38, 48]. Simulation studies taking cognizance of synaptic delays in

complex networks of interneurons have shown that the speed of moving waves is in the range of several cm/sec [27, 28], i.e., a very low speed. The detailed study of Cooper and Mundy–Castle [31], using spiral scanning toposcopy, showed that the moving wave of the alpha rhythm propagated from the occiput to the frontal area at a mean speed of 5 m/sec, with a range of 1–20 m/sec.

In the present study, the speed varied very strongly – from 1 to 50 m/sec and, further, to complete synphasicity over large areas (Fig. 2; see Table 1). The observations included very low seeds – mainly for the alpha and theta rhythms. Calculation of the data in Table 1 for the alpha rhythm puts the lowest speed at about 2.5 m/sec and gives an average of about 10 m/sec. We believe that this is in good numerical agreement the published data cited above. It is logical to suggest that at least some of the phase shifts measured in our study arose because of physiological propagation of oscillations across the cortex.

Simulation of the physical induction of oscillations, contrary to the above points, suggests potential propagation speeds an order of magnitude higher, i.e, not meters per second but tens of meters per second. Our studies are consistent with these data. A number of measurements revealed both very high potential wave movement speeds (for polyrhythmic oscillations and rapid oscillations) and complete synphasicity (instantaneous propagation) (Fig. 2; see Table 1).

Simulations of standing waves indicate a virtually instantaneous propagation of potentials across the cortical surface [32, 34]. In addition, Nunez [38] showed that the main properties of the temporospatial patterns of rhythmic electrical activity in the human brain may result from standing waves – a phenomenon arising from the interaction of traveling waves propagating in opposite directions. The antiphasicity of frontal and occipital waves described above in fact also represents instantaneous frontal-occipital propagation, while the variable local phase shifts in both halves of the head are reduced to distortions in wave shape, i.e., this appears to be the variant described by Nunez [23, 33, 37, 49].

Selection between physiological coordination and physical induction requires an answer to the question of the extent to which the EEG is local or the question of the electrical transparency of the brain. Low-intensity electrical fields are known to fade quite quickly in the substance of the brain – at distances of a few millimeters [13, 24, 29, 37]. Additionally, observations on cortical slices yielded three main conclusions: 1) the insignificant role of volume conduction in the propagation of cortical activity; 2) the primary role of the cortex in maintaining synchronization (of generator elements); 3) a tight correlation between the moving wave and the synchronization of elements [23, 42].

However, a whole series of factors suggest a high level of transparency of the brain for electrical fields and the reality of the physical induction of oscillations; for example,

the data cited above on standing waves and data from the equivalent dipole method [5, 8, 46]. This would appear to assume the simultaneous presence in the brain of both strong fields and currents influencing all electrodes and weak fields which are only locally apparent. Oscillations of these two types interact at each point.

In all our recordings, the speed changed in a wavelike fashion, forming apparent groups of waves. These were apparently identical to the "intervals of structural homogeneity" of oscillations described in the literature, where the phase structure is maintained essentially constant from wave to wave. Individual intervals succeed each other quasiperiodically with a frequency of 1–2 Hz [23] (see Table 1). It is interesting that simulation of sequential relay excitation of pyramidal cells yielded moving waves progressing at speeds of about 0.6 m/sec. Interference between standing and moving (in the pure sense) waves leads to wave groups with speeds of 0.6–32 m/sec, which is comparable to the effects of physical induction [52]. Overall, contemporary investigators usually note that oscillations in the EEG and magnetoencephalogram (MEG) generally behave as superimposed oscillations generated in different and possibly independent areas of the cortex [46].

The fact that local interelectrode phase shifts (the inverse of the speed) are strongly "bound" to the dominant oscillation frequency in a given area of the cortex requires separate discussion. Low-frequency activity is characterized by large absolute (msec) phase shifts from electrode to electrode as compared with high-frequency activity. This points indirectly to physical induction. The mechanism of this relationship is presumptively that variable current dipoles arise in the cortex, these being compact in size. Thanks to some degree of electrical "transparency" of brain tissue, these operate as sources of potential waves in several neighboring electrodes. The lag in induced oscillations expressed in terms of fractions of the period should increase with increases in the distance between the electrode and the source, because of the increase in the impedance of brain material between the source and the electrode (see the formula for the phase angle between a current and a potential for circuits containing a capacitance and a resistance [11, p. 42]). Lags expressed in units of time should increase more with greater oscillation periods (defined by the source), as observed in the present study.

Following this logic, the direction of the phase gradient reflects the current density gradient in the cortex, which is parallel to the surface, and, in conditions of multielectrode recording, can be used to locate compact sources lying close to the surface. The "foci" and "funnels" described here appear to be located above such current sources.

According to the data obtained by Rappelsberger et al. [44], there are morphological structures which behave as electrical dipoles (which contradicts the data cited above from slices) [42]). Interpretation of these indicates that the

electrical field from a current source with equal numbers of positive and negative charges weakens in the same way as a field generated by a current dipole, with the condition that the distance between the source and the measurement point must be much greater than the size of the source (the dipole). On this principle, dipole simulation is widely used as a method for locating sources to solve the reverse task. This is very useful for describing different types of electrical activity and yields meaningful results. However, Rappelsberger emphasizes that most of these "dipoles" are only equivalent dipoles. Dipoles can in fact be very local, but can also be distributed over large areas of nervous tissue [44].

The nature of these dipoles may be indicated by the following data. In our view, a model of a double electrical layer in the cortex as the source of current has the greatest potential for explaining these observations. Recording of early short evoked potentials in different cortical layers of the rabbit visual cortex using multiple electrodes allows the layered distribution of current source density to be recognized. Excitation of specific afferents leads to the appearance of an active current flow (electronegativity) in the depth of the cortex at the levels of layers 4 and 6, and then at the levels of layers 2 and 3. This involves the formation of the corresponding superficial passive current efflux (electropositivity) [44]. Supin [19] has performed an analogous study involving layer-by-layer analysis of the same evoked potential in the rabbit visual cortex, but only for a different component of the evoked potential – the slow inhibitory wave, which Supin regards as an exact analog of the alpha rhythm wave. The slow wave (and the alpha wave) also has a clear dipole nature and the form of a double electrical layer, though of the opposite polarity. "Negative polarity on the surface and positive polarity in the deep layers is evidence that the major current source (electropositivity) is located in the depth of the cortex, while passive flows of synaptic currents (electronegativity) occur predominantly in the upper layers" [19, p. 84]. Analogous data have been obtained in studies of spontaneous and evoked activity in cats [30].

All authors note such vertically oriented dipoles in relation to neuroanatomy. The role of cortical pyramidal cells in EEG electrogenesis is generally recognized [14, 15, 42]. This allows the model of a double electrical layer to be regarded as essentially universal for the cortex. Applying it to our results leads to the suggestion that most of the local phase shifts measured between neighboring electrodes are due to this mechanism. This refers to physical induction at several closely located electrodes from compact "planar" dipoles in the layer of the gray matter. The electrode closest to the dipole shows the most leading oscillation. Wave delays increase as the distance from the dipole increases. If the planar dipole occupies a significant area, then two (or more) electrodes can be located above it. Each of these points should show synphasicity. It is logical

to expect that increases in ascending thalamic activation of the cortex (synaptic bombardment) should lead to increases in the size (by power) of planar current sources. The areas of zones of synphasic oscillations should increase correspondingly, as in fact observed with increases in activation (Fig. 2). The largest synaptic currents should occur at the locations at which thalamocortical projections are densest. This apparently leads to the relationship seen between the foci of wave propagation and brain anatomy and their confinement to the geometry of the main projections, i.e., the visual, auditory, and somatic projections (see above).

The appearance of very powerful synaptic currents, characteristic of the visual zone [5], in the occipital area can lead to the appearance of the antiphasicity between the occipital and frontal poles described here, this distorting the "intrinsic" local phase structure in all other areas.

Published data as a whole show that brain electrical activity has a multiplicity of generators of different types, these being relatively independent of each other [10, 46, 50]. The results of our study add that activation of the cortex and sharp changes in the functional state alter the ratios of these sources, the ratios of different active EEG-generating mechanisms (physical induction and physiological coordination), and their relative contributions to generating the cortical rhythm at a given specific point.

CONCLUSIONS

1. The existence of a phase gradient in EEG oscillations across the area of the cortex is characteristic of all types of spontaneous electrical activity.

2. On activation of the cortex and increases in frequency, the rhythm of the phase shifts between neighboring electrodes in the corresponding zone decreases to the level of complete synphasicity.

3. The points giving rise to the initial appearance of EEG oscillations (with phase leadership) are confined to the anatomical locations of the main sensory projections – visual, auditory, and somatic.

4. It can be suggested that the direction of the local phase gradient reflects the current density gradient in the cortex, which is parallel to the surface.

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