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Modifications of EEG Related to Directed Perception and Analysis of Olfactory Information in Humans

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We recorded EEG in adult volunteers in the course of perception of smells of plant essential oils under conditions of directed attention. It was found that perception of olfactory information, even in the case of mild intensity of the smells inducing no aversive effects, correlates with noticeable changes in the EEG characteristics mostly typical of the reaction of nonspecific EEG activation induced by sensory stimulation and manifested in a decrease in the spectral power, SP, of low-frequency EEG components (6-10 Hz). In addition, the SP of relatively high-frequency EEG components (11-25 Hz) increased; this effect was most pronounced in the occipital regions of the neocortex. Perception of the smells of essential oils was also accompanied by increases in the coherence of EEG oscillations, most intense in the β_2 range (20-25 Hz). Such modifications were maximum in the left temporal/parietal region; this is interpreted as an indication of the special role of these cortical areas in the processes of interaction between the neocortical part of the olfactory analyzer and the respective structures of other analyzer systems. It is hypothesized that such interaction is necessary for the formation of a semantic image of the analyzed stimuli.

Keywords: EEG, olfactory stimulation, olfactory analyzer, spectral composition, coherence, essential oils, attention.

INTRODUCTION

Olfactory structures of the brain possess close morphofunctional connections with limbic structures [1] involved in realization of such “nonsensory” functions as the formation of emotions and memory [1-3]. The latter phenomena are considered crucial system-forming factors in the theory of functional systems [4]. In mammals, the cerebral cortex is the highest level for integration of different components of the functional systems and intersystemic interaction. At the same time, this level of the CNS is at present most completely examined from the aspect of its participation in the analysis of olfactory stimuli. Publications describing the pattern of modifications of electrical activity of the human brain (mostly changes in the characteristics of current EEG) under the influence of olfactory stimulation are fragmentary and, frequently, contradictory [1, 5-8]. It should

be noted that most authors, when estimating EEG modifications, limit themselves to an analysis of spectral power characteristics, while interpretation of the indices of distant synchronization of EEG oscillations is also necessary for estimation of the informational processes realized in the brain [9]. Close relations between olfactory and emotiogenic cerebral structures point to the existence of a few peculiarities of subjective perception of the smells; in particular, smells frequently possess clearly expressed emotional/hedonic estimates (“I like/do not like this smell”) [10, 11]. Noticeable specificities in the patterns of odorant-related changes in the EEG can result from the presence of an emotional factor [12, 13]. At the same time, we believe that some general patterns of activation of the brain in humans, which reflect different stages of analysis of olfactory information and do not depend on the smell type and its subjective estimate, should exist. Considering this, we carried out a study directed toward identification of general regularities of changes in the spectral power (SP) and coherence characteristics of cerebral electrical activity in humans, which were related to presentation of olfactory stimuli under conditions of oriented attention.

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METHODS

Sixty-seven students of the Kyiv institutes (18 to 25 years old, 24 women and 43 men, with no manifestations of rhinal pathologies) took part in the study as volunteers.

We recorded EEG in these subjects before, in the course of, and after perception of the smells of different plant essential oils (EOs). The use of olfactory stimuli of this class was related to the fact that humans rather frequently contact such substances, and smells of the latter are well known and habitual. Despite obvious interindividual variability of perception, these smells are, in most cases, qualified as pleasant and, much more rarely, as neutral or unpleasant, but with no significant aversive effect. We used EOs of lavender (*Lavandula officinalis*), rosmarine (*Rosmarinus officinalis*), ilang-ilang (*Cananga odorata*), Alpice pine (*Pinus alpinum*), lemon (*Citrus limonium*), mint (*Mentha piperita*), anise (*Pimpinella anisum*), bitter absinth (*Artemisia absinthium*), rose (*Rosa* sp.), and valerian alcohol potion (*Valeriana officinalis*). Small amounts of these liquids were dropped on strips of filter paper (50 × 10 mm) and put into tubes used in chemical semimicroanalysis (75 × 10 mm). Doses of the odorants were, as a rule, limited to one or two drops; they were selected in such a way that subjectively estimated intensities of the smells were nearly identical and sufficient for their detection and identification.

We tried to equalize the influences of the smell type and its subjective estimate on the results of the tests; for this purpose, subjects were asked to select two odorants from the above-described set, which were considered by this individual as the most and the least pleasant ones. Such a preliminary subjective estimation of the smells preceded recording of EEG; these two stages of the tests were carried out within different days. We should emphasize that any of the proposed olfactory stimuli was not estimated as clearly aversive (evoking disgust) by all the tested subjects (with no exception). This conclusion was supported by the pattern and level of changes in the indices of variability of the heart rhythm in these subjects observed in our preliminary study [14].

During EEG recording, the subjects were in a soundproof dark chamber, in a comfortable armchair in a reclined position, with their eyes closed. Before the test, closed tubes were put in a mobile support and positioned at such a distance from the subject (50 cm) that they were accessible, but perception of the smell was impossible. Then, the subjects were informed about their actions in the course of the experiment.

The experimenter left the chamber, closed the door, and switched off illumination. After adaptation of the subject to the recording conditions and recording of an EEG background sample (3 min), he/she received a voice command from the experimenter that he/she should open the first tube and position the latter, by moving the support, at a distance from the face (1 to 5 cm) allowing him/her to clearly perceive the smell of the test substance in the tube. The successfulness and accuracy of manipulations were provided by preliminary training (moving and opening of the tubes containing no odorant, in the illuminated chamber). After termination of manipulations with the tubes and other motor activities, the subject informed the experimenter, and, after a 15- to 30-sec-long interval, recording of EEG during perception of the smell of a definite odorant was begun (3 min long). Then, according to the voice command of the experimenter, the subject should close the tube and move it aside from the face (by moving the support). After this stage, a 3-min-long EEG sample was again recorded after termination of the movements. Each subject was asked to test three tubes in the following order: (i) the most individually pleasant smell, (ii) control (distilled water), and (iii) the least pleasant smell. Such a fixed order of smell presentations was determined by the psychological peculiarities of perception of “emotionally colored” stimuli. As is believed, the effect of a negative emotional influence is manifested for a longer time than that of a positive one. Before termination of the experiment, the subjects obtained no information on the contents of the proposed tubes. After testing of one odorant or another, a questionnaire developed in our laboratory was proposed to the subjects, and they should characterize the stimuli. This technique and analysis of its application were described in our earlier paper [11]. Intervals between trials with different odorants and control trials were not shorter than 3 min. Ventilation of the chamber in the course of the experiment was provided by an electric ventilator and opening of the door during filling of the questionnaire form. Thus, we believe that the sensory influence of the odorant presented in one test on the results of the next test was negligible.

Signals of EEG were recorded from symmetric frontal (Fp1, Fp2), parietal (P3, P4), occipital (O1, O2), and temporal (T3, T4) loci according to the international 10-20 scheme using a standard electroencephalograph. Interconnected ear contacts were used as a reference electrode. The interelectrode resistance did not exceed 5 kΩ. A high-frequency filter with a 70 Hz cut-off frequency and a power

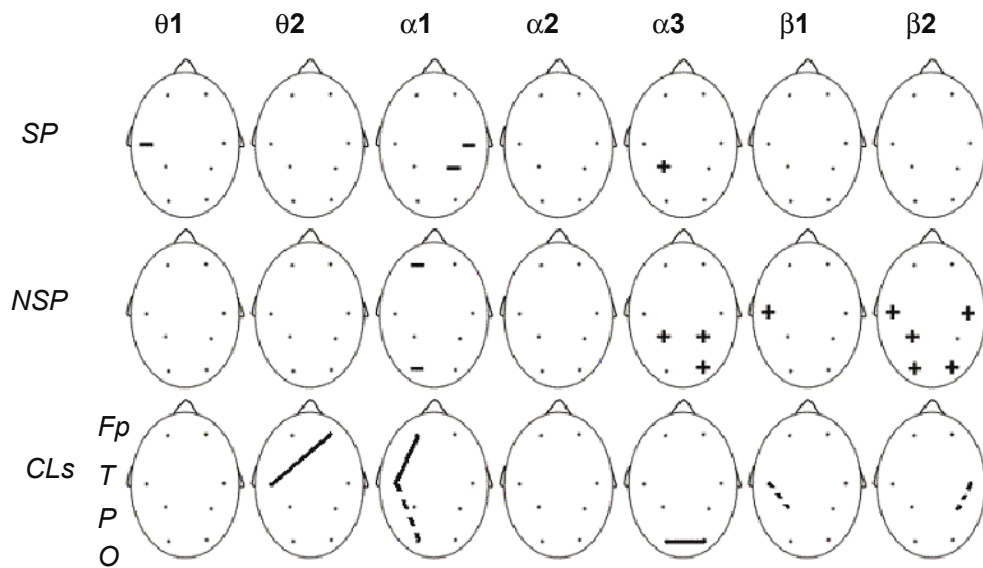


Fig. 1. Mapping of changes in the EEG parameters related to presentation of a control tube with distilled water to the subject (within the studied group, $n = 46$). Analyzed EEG subranges are indicated above the schemes. Symbols “+” and “-” show cases of significant ($P < 0.05$) increases or decreases in the values of spectral power (SP) and normalized SP (NSP) in one lead or another. Solid lines connect pairs of leads where a significant increase in the coherence levels (CLs) was observed, while dashed lines connect leads where the CLs decreased. Fp, T, P, and O indicate loci of the leads.

network filter (50 Hz) were used; the time constant of the amplification tract was 0.3 sec. Signals from the encephalograph were digitized at a 100 sec^{-1} frequency and entered into a PC. Within each 3-min-long interval (background, perception of the smell, and aftereffect), we recorded six 20-min-long EEG segments. The records were subjected to preliminary visual control of the quality, and 15-sec-long artifact-free realizations were selected. Using a special software based on an algorithm of fast Fourier transform, SPs of seven frequency subranges were calculated for these EEG samples. These were low- and high-frequency components of the theta rhythm ($\theta 1$, 4.0 to 6.0 and, $\theta 2$, 6.0 to 7.5 Hz), low-, medium-, and high-frequency components of the alpha rhythm ($\alpha 1$, 7.5 to 9.5, $\alpha 2$, 9.5 to 11.0, and $\alpha 3$, 11.0 to 13.0 Hz), and low- and high-frequency components of the beta rhythm ($\beta 1$, 13.0 to 20.0, and $\beta 2$, 20.0 to 25.0 Hz) [15]. We also calculated the mean levels of coherence (LCs) for oscillations of the above ranges for all 28 possible pairs of the leads. In addition, we calculated normalized SP values (NSPs) for the above ranges (ratios of the SP of a definite range vs the integral power of EEG oscillations within the entire set of the above-mentioned ranges taken as 100%). The analyzed epochs were 5.12 sec long, and the epochs of averaging were equal to 1/8 of the analyzed epoch.

We tried to identify the general patterns of EEG

modifications related to the analysis of olfactory information; for this purpose, all EEG samples recorded in the course of testing the actions of odorants were gathered in single samplings. One hundred-one samples of EEG reactions to presentations of the smell (of 134) and 46 reactions to presentations of the control tube with distilled water (of 67) were found to be acceptable for the analysis (according to the quality of records). In this study, we did not take into account such factors as subjective estimates of the stimuli and gender and psychotypical peculiarities of the subjects. Our further studies will be aimed at the analysis of these aspects. In each case, numerous EEG indices were analyzed; these were SPs of seven frequency components recorded from eight leads (i.e., 56 values), 56 values of the NSPs, and 196 values of the CLs; all these figures were characterized by natural interindividual variability. This is why we limited ourselves to an analysis of the qualitative aspect of the changes (their presence or absence, and their direction, i.e., increase or decrease). The significance of differences between the examined parameters at comparison of the interdependent samplings was estimated using a Wilcoxon's criterion of sign range sums. Differences between qualitative characteristics of changes in the parameters of EEG recorded from different leads were estimated using a nonparametric version of single-factor analysis (Kruskal-Wallis

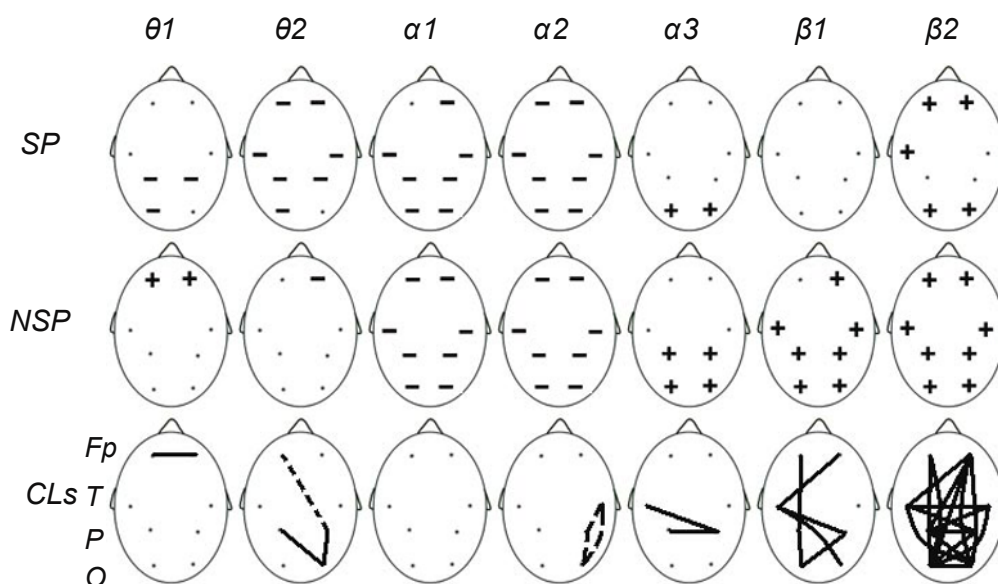


Fig. 2. Mapping of changes in the EEG parameters related to presentation of olfactory stimuli (tubes containing samples of plant essential oils, $n = 101$). Designations are similar to those in Fig. 1.

criterion). These calculations were performed using Statgraphics 5.1 software (Manugistics, USA) and macroses, which were realized using Visual Basic for Applications programming language (Microsoft Excel software).

RESULTS

Analysis of the results obtained showed that only a small number of presentations of a tube with distilled water led to changes in the EEG parameters (Fig. 1). Within the studied group, 4 of 56 shifts in the SP values, 11 of 56 those in the NSP, and 6 of those in the CL were found to be significant. In general, decreases in the SP of oscillations of the θ_1 subrange and in those of the α_1 subrange were observed in leads P4 and T4. Analysis of the NSP changes showed that the proportion of high-frequency EEG components increased somewhat. In the occipital/parietal regions, α_3 oscillations were augmented; in the occipital/parietal/temporal leads, the power of β_2 oscillations increased, while β_1 oscillations in the left temporal region became stronger. Changes in the CL were mild and topographically irregular (Fig. 1). Comparison of the levels of changes in the SP within one range but in different leads showed that the increment of this index for the β_2 range in lead T3 was significantly greater ($P < 0.05$ when compared with the indices for Fp1, Fp2, P3, and P4).

In contrast, perception of the oil smells by the tested subjects was accompanied by considerable modifications by the current EEG (Fig. 2). Thirty-two of 56 shifts in the SP, 38 of 56 in the NSP, and 31 of 196 in the CL were found to be significant. For the group in general, significant decreases in the SP of 6 to 11 Hz oscillations were typical. Such a decrease was observed for α_2 oscillations in all leads, those for α_1 and θ_2 oscillations were found in all leads except for one, while for oscillations of the low-frequency θ subrange this was observed in leads P3, P4, and O1. At the same time, the SPs of relatively high-frequency EEG oscillations increased somewhat. The α -range power increased in leads O1 and O2, and that of the β range became greater in leads Fp1, Fp2, T3, O1, and O2. Changes in the NSP values in general corresponded to those in the natural SP values.

Comparison of the intensity of changes in the SPs of the θ_1 range showed that maximum shifts of this index were observed in the Fp1 and Fp2 leads ($P = 0.01$ according to the Kruskal–Wallis criterion and $P < 0.05$ in paired comparison with other leads). For the θ_2 range, such shifts were the greatest in lead T3 ($P < 0.05$ when compared with O2); for the α_3 subrange, this was observed in O1 and O2 ($P = 0.017$ by Kruskal–Wallis and $P < 0.05$ in paired comparison with other leads), and for the β_2 subrange, the maximum differences were found in T3, O1, and O2 ($P = 0.03$ by Kruskal–Wallis and $P < 0.05$ in paired comparison with other leads) (Fig. 2).

TABLE 1. Mean Ranges of Changes in the Coherence Levels (CLs) of Oscillations of the β_2 Subrange Related to Perception of the Smells of Essential Oils by the Tested Subjects

Lead pairs	Mean range	Lead pairs	Mean range	Lead pairs	Mean range	Lead pairs	Mean range
Fp1 – Fp2	1247	Fp2 – P3	1444	P3 – O1	1414	P4 – T4	1220
Fp1 – P3	1546 *	Fp2 – P4	1441	P3 – O2	1492	O1 – O2	1524
Fp1 – P4	1421	Fp2 – O1	1457	P3 – T3	1230	O1 – T3	1277
Fp1 – O1	1450	Fp2 – O2	1424	P3 – T4	1566 *	O1 – T4	1433
Fp1 – O2	1320	Fp2 – T3	1464	P4 – O1	1439	O2 – T3	1563 *
Fp1 – T3	1371	Fp2 – T4	1301	P4 – O2	1403	O2 – T4	1378
Fp1 – T4	1391	P3 – P4	1439	P4 – T3	1553 *	T3 – T4	1400

Footnotes. Changes in the CLs were calculated as differences between the values of this index in the course of perception of the smell and in the initial state divided by the initial CL value. The procedure of ranging was performed for the data of all individual experiments; the table shows mean ranges for each pair of the leads. Asterisks show lead pairs where changes in the CL were the maximum (a statistically significant difference in paired comparison with the smallest values).

TABLE 2. Summarized Ranges of Changes in the Coherence Level of β_2 EEG Oscillations in the Course of Perception of the Smells of Essential Oils by the Examined Subjects

Lead	Summarized ranges
F _{p1}	9746
F _{p2}	9778
P3	10129
P4	9915
O1	9993
O2	10105
T3	9857
T4	9688

Significant changes in the indices of spatial synchronization involved mostly high-frequency EEG components (25 of 32 significant changes of the CLs). The CL values increased for two pairs of the leads in the α_3 range, for five pairs in the β_1 range, and for 18 pairs in the β_2 range. Considering the relatively high intensity of changes in the CL of β_2 oscillations, we tried to calculate their quantitative estimate. As was found, changes in the CLs were the maximum in the following lead pairs: Fs–Ps, Ps–Td, Pd–Ts, and Od–Ts (Table 1; $P = 0.07$ by Kruskal–Wallis and $P < 0.05$ in some paired comparisons).

In addition, we were interested in the question of what examined region of the neocortex manifests the greatest changes in the spatial synchronization of EEG. This is a rather ambivalent, from the mathematical aspect, question, because indices of spatial synchronization are calculated for pairs of leads but not for each lead separately. To answer this question, we calculated integral ranges of the CL changes for all pairs including one lead or another and compared the indices obtained (in fact, we added to each other the values shown in Table 1 for all pairs, including the given lead). When using such an approach in calculations, the greatest range was found

for the left parietal lead, i.e., for P3 (Table 2). Thus, we can hypothesize that just this cortical region is, in a certain sense, a center of integration in the analysis of olfactory information.

DISCUSSION

According to the hypothetical model proposed by Lorig [5], the functional system responsible for perception of olfactory stimuli is composed of the modally specific sensory structures, emotigenic structures (their role is estimation of the biological value of the stimuli analyzed), and structures providing semantic analysis of the incoming information and processes of selective attention. The latter structures are probably also involved in verbal identification of the smells and their hedonic properties and are responsible for the processes of association of the stimuli with stimuli of other modalities [5]. Naturally, activation of the mentioned components of the olfactory analyzer should be reflected in alternations of the neocortical electrical activity. Analysis of our data carried out within the context of the above-described scheme showed the following.

A definite decrease in the power of θ -range EEG oscillations was found to be one of the most clearly pronounced odorant-dependent modifications of the cerebral activity (Fig. 2). Comparable findings were also described by other authors that analyzed perception of some smells [6]. At the same time, a number of reports noted that an increase in the SP of this range is related to activation of attention [16, 17]. Considering these data, Martin concluded that the level of attention in humans decreases at perception of definite smells [6]. We believe that such interpretation is not completely correct. The action of

all sensory stimuli should lead to an increase in the level of attention directed toward the stimulus source [18]. It should be taken into account that the task proposed to the subjects in our experiments included targeted perception of the smells and their subsequent estimation. Thus, the experimental conditions required certain concentration of attention by the subjects on the stimuli applied. After the beginning of the tests, the subjects expected the experimenter's command. Therefore, a definite part of their attention was directed to the auditory signals; this circumstance was a potential reason for some drop in the level of attention. After opening of the tube, attention was switched for perception of olfactory information, and the net effect of activation of the attentive mechanisms could be, in this case, negative. Nonetheless, our control tests showed no decrease in the SP of the θ rhythm, which could be related to opening of the tube (Fig. 1); thus, the above-described changes in the SP of this EEG frequency range can be considered specific for analysis of the action of olfactory stimuli.

A certain decrease in the emotional tone of the tested subjects [19], their relaxation induced by the action of odorants, can be another interpretation of the observed decrease in the SP of θ oscillations. At the same time, such interpretation cannot be adequate with respect to all subjects because many of them characterized the proposed smells in their verbal reports as "activating" or "excitatory" [11]. Thus, when summarizing the above-described data, we can conclude that the observed phenomenon of suppression of the θ 2 range upon the action of olfactory stimuli needs further investigation.

In addition, some rise in the NSP of the θ 1 range in frontal zones deserves attention. This effect was accompanied by an increase in the level of spatial synchronization in these regions. Considering that just the frontal cortical zones are believed to be important components of the substrate responsible for selective attention [18, 20] and memory [21], we can suppose that a rise in the proportion of θ 1 oscillations in the resulting EEG is related to activation of the above mechanisms. The relatively mild intensity of these changes (the absence of increment in the natural SP values) can be interpreted in such a way. It was reported that significant increases in the amplitude of θ oscillations accompanied the performance of specialized tasks with active involvement of the mechanisms of selective attention and memory. In our tests, the subjects had no such tasks; consequently, the level of involvement of such mechanisms was not very high.

According to our observations, peculiarities of modifications of SPs of different subcomponents of the α rhythm in the course of perception of the smells of plant EOs show that two functionally different components are probably present in this EEG rhythm.

As was mentioned above, action of the olfactory stimuli resulted in decreases in the SPs of the α 1 and α 2 subranges in all leads (Fig. 2). Such an α desynchronization can be a manifestation of nonspecific activation of the neocortex related to sensory stimulation. Some authors interpret a decrease in the power of the low-frequency α rhythm as an effect induced by activation of the attention mechanisms [21]. Such a supposition agrees with the above-described interpretation of changes in the SP of the θ 1 range in the frontal leads.

At the same time, the dynamics of the SP of the high-frequency α -range component was found to be opposite. In our experiments, modulation of the α 3 range appeared closer to that of the β EEG rhythm but not to that of other subranges of the α rhythm. It is believed that intensification of high-frequency components of EEG is related to activation of the cognitive mechanisms [22]. The paradigm of our tests required a relatively high-level semantic analysis of the proposed stimuli by the subjects and, therefore, the involvement of the associative neocortical regions. This was probably reflected in increases in the SP of the β 2 activity in the frontal/temporal regions. At the same time, according to changes in the SPs of the α 3 and β 1 subranges, activation of the occipital cortical regions dominated in this case, and this should be considered as a somewhat paradoxical effect. It seems that neocortical structures of the visual analyzer are involved in the analysis of olfactory information. We should note that the right occipital region occupied the second position according to an increase in the coherence (after the left parietal region) (Table 2). It is interesting that the participation of occipital regions in the processing of olfactory information was also demonstrated in tomographic studies [3]. As is believed, this fact can reflect the formation of mental visual images related to the action of odorants.

It should be mentioned that a noticeable (but less intense) increment of the SP of high-frequency EEG components was also observed after presentation of control "stimuli" (Fig. 1). This fact can probably be interpreted as related to the cognitive predisposition of the subjects to detection of a smell formed before the beginning of the experiment. Because of this, cerebral mechanisms "searched" for the expected stimulus even in the absence of the latter. Data on the

influence of the cognitive disposition on the pattern of subjective perception of olfactory stimuli [23] are of interest from this aspect. It seems probable that such a situation was realized in our tests. Activation of the mechanisms of descending control can play the role of the substrate for this process. Such activation, as Sergin [24] believes, forms a definite sensory "prognosis" and leads to generation of the corresponding specific patterns of electrical activity related to transmission of the influences from "upper floors" of the CNS to the lower ones. The study of Mayberg et al. [25] is also interesting from this aspect. According to the conclusions of these authors, the placebo effect in medical practice is caused by modulation of the activity of some cortical and subcortical structures realized by "higher" cortical regions. Among such targets, limbic structures (prefrontal cortex, insula, and others) were mentioned in the cited paper; these structures are also involved in the analysis of olfactory information.

We observed one other phenomenon related to olfactory activation of the brain. This was an increase in the level of spatial synchronization of high-frequency EEG oscillations in many lead pairs and with the involvement of all examined neocortical regions (Fig. 2). A quantitative analysis of changes in the CLs of oscillations of the β_2 subrange (Tables 1 and 2) showed that the maximum increment of the level of spatial synchronization of EEG was observed in the left parietal/temporal zone. Functional domination of these cortical regions in the course of perception of olfactory stimuli was also demonstrated using detection of evoked magnetic fields (magnetic resonance imaging) [26] and recording of evoked chemosensory potentials [27]. Besides this, some researchers correlate increases in the coherence of high-frequency components of the EEG spectrum with the processes of interaction of neocortical representations of different analyzer systems. It has been mentioned that the dominating role in these processes belongs just to the parietal/temporal areas [28]. Thus, it is quite possible to hypothesize that the recorded odorant-dependent changes in the CLs of high-frequency EEG oscillations were manifestations of the processes of interaction between the neocortical representation of the olfactory analyzer with the respective structures of other analyzers. Such interaction is probably related to the formation of a semantic image based on the obtained sensory information. It should be mentioned that domination of activation of the left cerebral hemisphere was observed in this case; this hemisphere is to a greater extent involved in the verbally conditioned processes.

When analyzing odorant-dependent EEG modifications, it is interesting to compare the dynamics of indices of local and distant synchronization of high-frequency oscillations of the EEG spectrum upon presentations of a control stimulus and a real olfactory stimulus. An increase in the SP of the above oscillations was a general phenomenon for both experimental conditions. At the same time, an increase in the CLs was observed only upon perception of the EO smells (Figs. 1 and 2). This is why we can suppose that changes in the SP are partially related to nonspecific sensory processes determined by activation of the mechanisms of detection of smells in the air, while changes in the CLs reflect processes of analysis of incoming actual sensory olfactory information.

Therefore, our study allowed us to identify some manifestations of activation of cerebral systems in humans, which are related to processing of olfactory information and probably reflect some processes of intermodal integration.

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