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Background Gamma Activity in the Electroencephalogram as a Measure of the Level of Sustained (tonic) Attention during Execution of the "Active Oddball" Paradigm in Rabbits

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Tonic brain activity has significant influences on the nature of a subject's responses to target sensory stimuli. We report here studies of the dynamics of the background activity in the gamma-rhythm range of the EEG in rabbits during execution of an "active oddball" paradigm modified for animals – a task widely used for studies of attention. Increased levels of power and coherence in background gamma activity were found to reflect expectation of a target stimulus, correct responses to stimuli being executed at a particular level of background gamma activity which probably corresponds to the optimum level of sustained (tonic) attention. Decreases in the level of gamma activity led to missed responses to the target stimulus, while excess levels lead to erroneous responses to non-target signals (false anxiety). These dynamics of background gamma activity are interpreted as resulting from oscillations in the level of tonic cholinergic activation of right cerebral cortex.

Keywords: attention, operant conditioned reflex, oddball, electroencephalogram, gamma rhythm, rabbit.

The defining role of the tonic activity of neural networks in supporting the body's appropriate responses to sensory stimuli has been demonstrated and analyzed in detail by recording spike activity from single neurons and low-frequency EEG activity in the range 4–10 Hz [3] during the formation and execution of conditioned reflex tasks of different levels of difficulty. Current physiological studies of brain activation, as well as attention and perception, made wide use of recording of the high-frequency component of the EEG spectrum – the gamma rhythm, i.e., oscillations of cortical potentials in the range 30–70 Hz and above [1, 2, 6, 14, 16, 18, 21].

Tonic gamma activity is known to change in accordance with the ongoing state of the subject and the task being executed. In particular, generation of gamma activity increases in the state of attention and/or mental loading. Thus, studies in 1980 showed that increases in the EEG gamma rhythm in cats occurred at the time point at which they paid full attention to their target prey [12]. Similarly, gamma rhythm power in humans increased during cognitive loading as compared with the resting state; gamma activity differed in this way from activity in the beta range – which, conversely, decreased when cognitive loading increased [20].

Existing data indicate that the level of background, i.e., spontaneous, gamma activity and the subject's response to sensory stimuli are related to each other. For example, psychophysical experiments have shown that correct responses to target stimuli are preceded by a higher background gamma level than missed responses to these stimuli [22]. Expectation of a stimulus and preparation to execute a reaction in response to a stimulus also lead to increases in gamma activity [2, 18]. On the other hand, episodes of significant increases and synchronization of the gamma rhythm to above the baseline level are accompanied by the so-called inattention blindness, in which responses to sensory stimuli are blocked [15].

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Thus, there is currently a set of experimental data showing that changes in the level of sustained, or tonic, attention (defined as a subject's readiness to make a response, appropriate to the conditions of the task, to discrete sensory stimuli over a long period of time) are accompanied by variations in measures of background gamma activity. Nonetheless, data on the phenomenology of this situation remain controversial and contradictory and its mechanisms virtually unknown.

The aim of the present work was to study the generation of background gamma activity in the EEG in rabbits in relation to variations in the level of sustained (tonic) attention during execution of the "active oddball" paradigm (a task widely used in studies of attention), including: 1) assessment of background gamma activity at different levels of sustained attention due to changes in the subjectively expected probability that the target stimulus will be presented; 2) assessment of the interaction between background gamma activity and the level of sustained attention influencing the correctness with which the target and non-target stimuli are recognized.

METHODS

Training of Animals and Recording of Behavior in Experimental Conditions

The experimental model based on the active oddball paradigm, developed by ourselves for animals, consists of differential conditioned reflex stimuli, one of which, the target (conditioned) stimulus, is presented significantly less frequently than the non-target (differential, ignored) stimulus. Having executed an operant movement in response to the target stimulus, the animal receives a drink as reinforcement; execution of a movement in response to the non-target stimulus is regarded as an error and is not reinforced [5]. The operant reaction to the target stimulus is developed by increasing the sequential components of the reflex behavior.

Experiments were performed in a screened light- and soundproofed chamber in freely moving rabbits weighing 3–4.5 kg. During experiments, animals were subjected to fluid deprivation without reducing body weight by more than 20% of initial. The animals' operant movements were that the forepart of the head had to break a light beam in the recording device on the floor of the pen. Correct movements performed within 4 sec of stimulus activation were reinforced by delivery of 5 ml of fruit juice from an automatic bowl also fixed to the floor of the pen close to the recording device (method developed by B. V. Chernyshev and Moskvitin). Sound stimuli were delivered via a loudspeaker located above the experimental pen; tone duration was 40 msec, with rise and decay times of 10 msec, and loudness was about 70 dB. For animals of group I (four rabbits), the target (conditioned) stimulus was a tone of 2000 Hz and the non-target (differential) stimulus was at 800 Hz; the same stimuli were used for animals of group II (four rabbits) but with the values reversed (target stimulus at 800 Hz, non-target stimulus at 2000 Hz). Use of two groups of animals allowed the effects of attention to be studied independently of differences in the physical parameters of the target and non-target stimuli. The target and non-target stimuli were presented in quasirandom order at a ratio of 1:4; two target stimuli never followed immediately one after the other and were always separated by at least two presentations of the non-target stimuli. Each experiment involved 150–450 trials (including 30–90 presentations of the target stimulus). The interstimulus interval was 8 ± 1 sec. During experiments, four variants of behavioral responses to stimuli were seen: positive reactions and missed reactions in response to the target stimulus, erroneous responses (false anxiety), and correct refusals to respond to the non-target stimulus.

Surgery and EEG Recording

Surgery to implant macroelectrodes for EEG recording was performed in a stereotaxic apparatus under general anesthesia (Nembutal, 55 mg/kg) and local anesthesia with 2% novocaine solution. Silver macroelectrodes for EEG recordings were placed on one side above the frontal (F), lateral parietal (lP), and central parietal (cP) areas of the cortex; macroelectrodes were implanted into bone to a depth of 1.5 mm at points with coordinates of $A = 7$, $L = 1$–3.5 for recording F; $P = 1$–2, $L = 5.5$-6 for recording lP; and $A = 0$, $L = 0$ (the bregma) for recording cP, using an atlas [7]. These recording points were selected on the basis that the frontal and parietal areas of the cortex are currently assigned a significant role in organizing attention [10, 23]; in addition, these cortical areas are those in which the P300 late cognitive potential is recorded, i.e., the most characteristic electrophysiological manifestation of brain activity in the oddball paradigm [26].

The reference electrode was positioned 10–15 mm anterior to the bregma, close to the sagittal suture, and the ground electrode was placed in the posterior part of the skull ($A = -10 \pm 2$, $L = 2 \pm 1$). All electrodes were fixed to bone with fast-setting resin, after which the animal's head was fitted with a 10-way socket. A multicore flexible screened cable was plugged into the socket for EEG recording, with low-noise repeaters. The EEG signal was then delivered to an ISDB biopotentials amplifier (WPI Inc., USA) and then to the analog-to-digital converter (ADC) of an L-305 input-output card (L-Card, Russia) fitted in a standard computer. EEG recordings were made with a time constant of 1.6 sec and an upper frequency cut-off of 70 Hz; the sampling frequency was 512 Hz. Experiments were controlled and recordings were made of the EEG and light beam crossing times automatically using the Emerald Spike program (by B. V. Chernyshev).

Analysis and Processing of Experimental Data

Artifacts were removed from EEG traces automatically and by visual assessment of traces for all trials. Gamma

TABLE 1. Mean Spectral Composition of Background Gamma Activity in the EEG of Rabbits on Execution of the Active Oddball Paradigm (mean ± ± standard error)

Frequency range, Hz	Power, %	Coherence
28–36	25.1 ± 0.4	0.393 ± 0.003
36–44	23.7 ± 0.4	0.397 ± 0.004
44–52	24.0 ± 0.6	0.422 ± 0.004
52–60	16.9 ± 0.4	0.405 ± 0.004
60–68	10.3 ± 0.2	0.375 ± 0.004
28–68	100.0 ± 1.7	0.399 ± 0.004

activity power and coherence were calculated in Emerald Spike over the range 28–68 Hz for 500 msec of prestimulus activity using fast Fourier transformation with a superimposed Hann window. Gamma activity parameters were calculated using non-averaged EEG traces.

Background activity was analyzed before non-target and target stimuli for each experiment. As each target stimulus was followed by a continuous sequence of a mean of four non-target stimuli, additional analysis of non-target stimuli was applied to trials in which the non-target stimulus was the first to be presented after a target stimulus (henceforth – first non-target) and trials in which the non-target stimulus was the last in the series presented before a target stimulus (henceforth – last non-target). In addition, background activity was analyzed separately before positive responses, missed responses, erroneous responses (false anxiety), and correct refusals to respond. In general, each such analysis included 25–90 trials from one experiment; in the case of erroneous responses to non-target stimuli, which were relatively rare, analysis was performed only when there were at least six behavioral errors in one experiment. In all cases, the correctness of calculations for paired comparisons of gamma activity parameters was verified by using equal numbers of trials in the two situations within a single experiment. Statistical comparisons were performed using the nonparametric Wilcoxon and Mann–Whitney statistic run on Matlab 6.5 (Math-Works Inc., 2002) and Statistica 6.0 (StatSoft, Inc., 2001).

Animal studies were performed in accordance with USSR Ministry of Higher Education decrees No. 742 of 11.13.84, "Approval of regulations for studies with experimental animals," and No. 48 of 01.23.1985, "Control of studies using experimental animals."

RESULTS

Gamma activity was recorded in 148 experiments on eight rabbits (groups I and II, each of four animals).

Spectral Composition of Background Gamma Activity

Analysis of gamma-rhythm power spectra showed a relatively uniform distribution over the whole of the study range 28–68 Hz, with very minor predominance of power in the low-frequency half of the spectrum (Table 1). Results obtained from analysis of the whole gamma-activity range overall are presented, as similar analyses performed for sequential narrow bands of the spectrum over this range revealed no significant patterns differing from those presented below.

Dynamics of Background Gamma Activity Depending on Stimulus Targetness

During execution of the active oddball, the power of background gamma activity was greater before target than before first non-target stimuli ($p < 0.001$ for both groups and all leads; Fig. 1, *A*, *B*). This means that after presentation of a target (reinforced) stimulus, there was a stable decrease in the level of background gamma activity. Gamma activity preceding last non-target stimuli also showed a lower mean level than before target stimuli, though this difference was not as significant and reached the significance level only for the cP lead (Fig. 1, *A*, *B*).

On the other hand, background activity before last non-target stimuli was very significantly elevated as compared with background activity preceding first non-target stimuli ($p < 0.001$ for both groups and all leads; Fig. 1, *A*, *B*).

Analogous highly significant differences were also seen in both groups of animals in relation to coherence between the cP lead and two other leads, i.e., the F–cP and lP–cP pairs (Fig. 1, *C*, *D*): coherence levels between these leads were significantly greater before target than before first non-target stimuli and before last non-target stimuli than before first non-target stimuli. In the lead pair F–lP, there were no clear significant patterns.

Thus, both power values (in all leads) and coherence (between lead cP and the other two leads) increased significantly as the number of non-target stimuli in the sequence increased and the subjectively expected probability that a

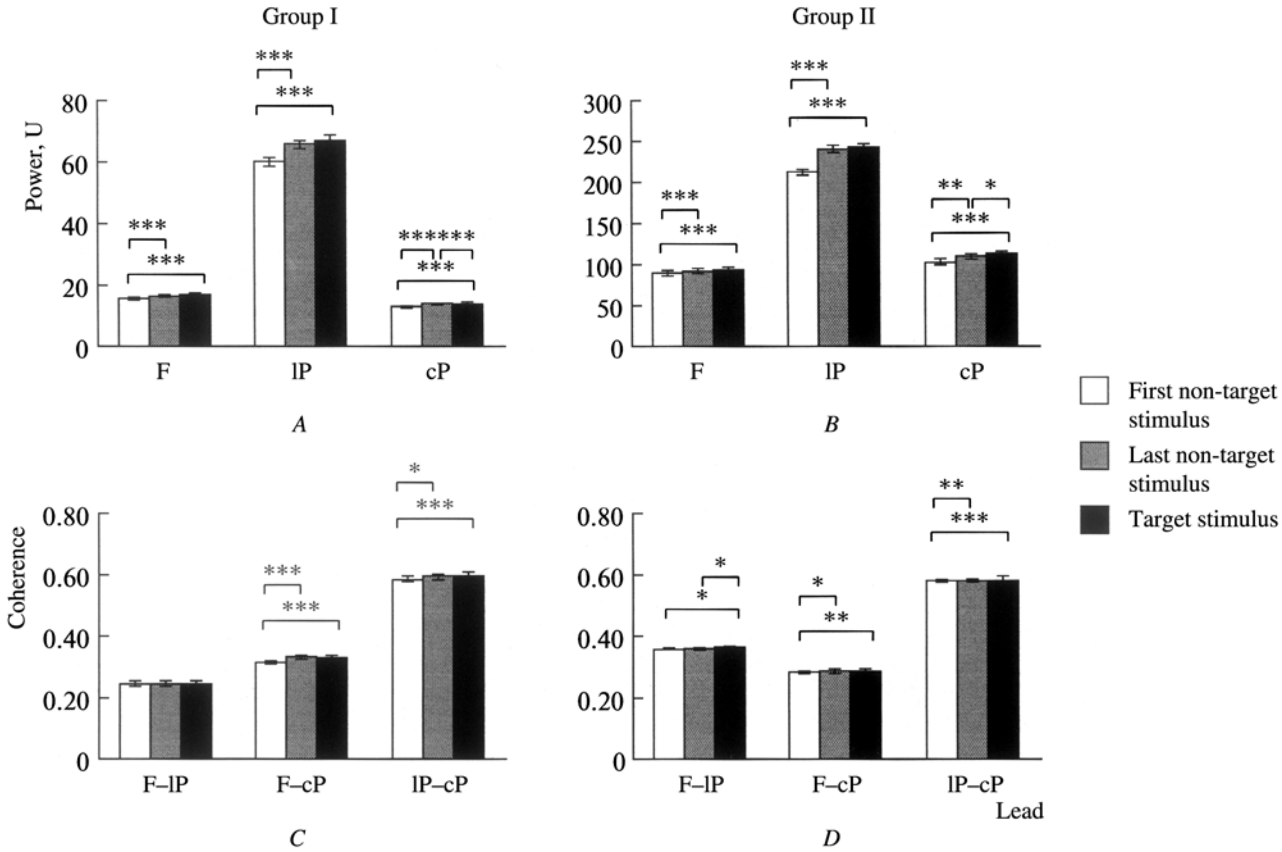

Fig. 1. Background gamma activity before presentation of non-target and target stimuli. *A*, *B*) Gamma activity power in groups I (*n* = 52) and II (*n* = 96); *C*, *D*) coherence of gamma activity in groups I (*n* = 52) and II (*n* = 96). F – frontal lead; lP – lateral-parietal lead; cP – central-parietal lead. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, Wilcoxon's test; brackets above columns show the pairs of values being compared. Here and henceforth, data are plotted as mean ± ± standard error.

target stimulus would be presented next increased in the oddball paradigm; values reached maximal levels immediately before presentation of the target stimulus. After presentation of a target stimulus, these measures again "discharged" to lower levels, when the expected probability that the next stimulus to be presented would be target in the experimental paradigm used here was close to zero.

Background Gamma Activity before Execution and Non-Execution of Operant Movements

Power levels of background gamma activity were significantly greater in all leads in both groups of animals before execution of an operant movement in response to the target stimulus (positive responses) as compared with missed responses to the same stimulus ($p < 0.001$ for both groups and all leads; Fig. 2, *A*, *B*). For coherence, an analogous pattern for background gamma activity was seen in animals of both groups in the lead pair lP–cP (Fig. 2, *C*, *D*).

Comparison of the situations in which execution and correct non-execution of the operant reaction in response to the non-target stimulus gave similar results: the power of background gamma activity was significantly greater before execution of erroneous movements to non-target stimuli (false anxiety) as compared with correct refusals to execute movements in response to the same stimulus ($p < 0.01$ for both groups and all leads; Fig. 3, *A*, *B*).

Thus, movement (both positive and negative reactions) were executed in those cases in which the power (and particularly coherence) of spontaneous background activity before the moment of stimulus activation was greater.

Background Gamma Activity before Correct and Erroneous Execution of the Operant Reaction

The data presented above indicate that overall, the level of gamma activity before target stimuli was greater than that before non-target stimuli. Comparison of these two situations of movement execution – correct and erroneous – showed that before erroneous reactions to the *non-target* stimulus (false anxiety), background activity in all leads in both groups was greater than before correct (positive) reactions to the *target* stimulus (Fig 3, *A*, *B*). This difference was significant and most marked for lead lP ($p < 0.05$ for both

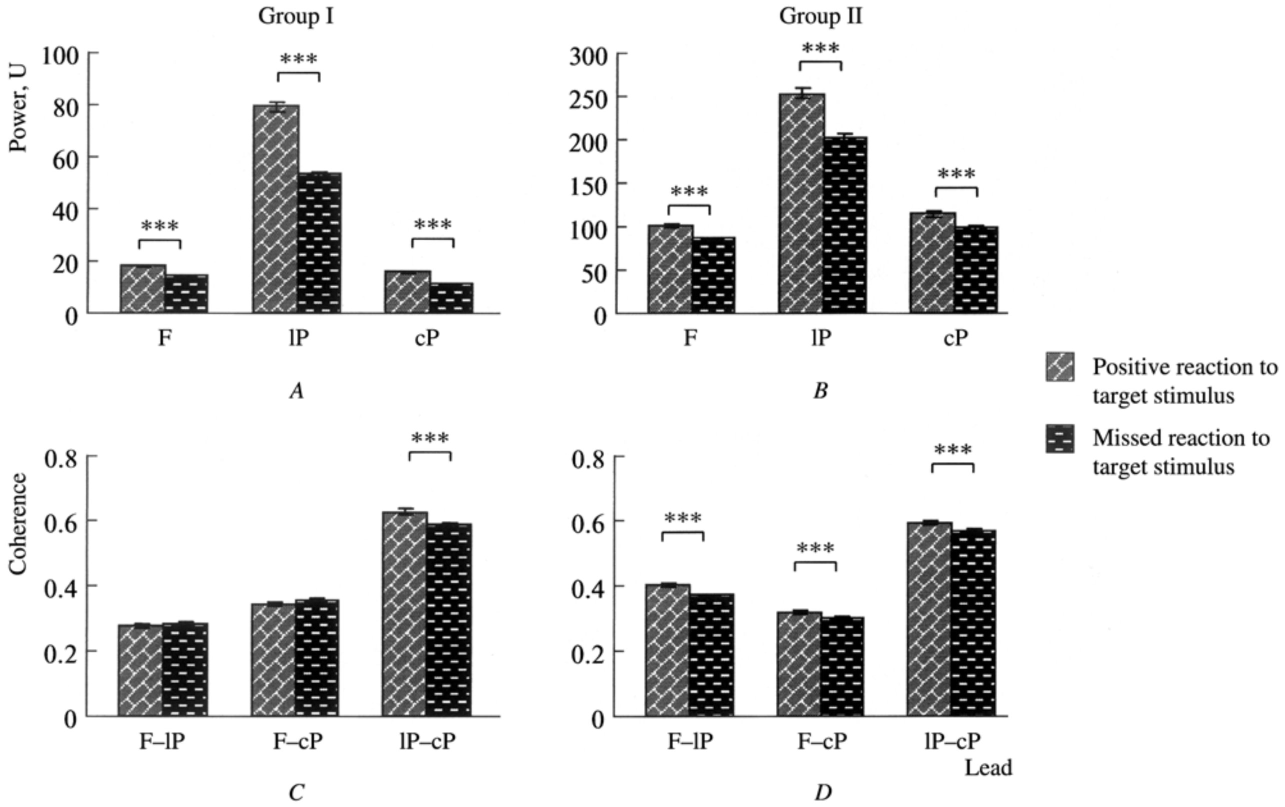

Fig. 2. Background gamma activity before presentation of target stimuli with positive operant reactions and missed reactions. *A*, *B*) Gamma activity power in groups I ($n = 50$) and II ($n = 84$); *C*, *D*) coherence of gamma activity in groups I ($n = 50$) and II ($n = 84$). For further details see caption to Fig. 1.

groups). It should be noted that this comparison was performed using a relatively small sample set ($n = 13$ in group I and $n = 27$ in group II), as the analysis included only those experiments in which at least six erroneous reactions to the last non-target stimulus were executed. In relation to the coherence of gamma activity, this analysis did not allow any visible patterns to be detected (Fig. 3, *C*, *D*).

Thus, the power of background gamma activity before execution of erroneous reactions to the non-target stimulus was significantly greater than before positive reactions to the target stimulus.

DISCUSSION

The present study used the “active oddball” paradigm as modified by ourselves for animal experiments [5]. Stimulus characteristics and behavioral requirements were analogous to those used on execution of the active oddball in humans [4, 26, and others], which allows our results to be compared with published data obtained in human studies. In contrast to similar experiments on humans, where subjects are usually able to discriminate reliably between target stimuli and non-target stimuli with virtually no errors, our studies allowed assessment of variations in the level of attention within a single experiment in terms of the animal’s behavioral reactions to stimuli and analysis of background gamma activity on missed reactions and false anxiety.

The question of whether the gamma activity recorded in our experiments was actually generated in the animals’ brains is important. One potential source of electrical oscillations in the gamma range is the olfactory bulbs, as the reference electrode was located relatively close to these structures. Nonetheless, control traces in which the EEG was recorded relative to lead lP or the ground electrode (located in the posterior part of the skull) rather than the standard reference electrode showed that gamma activity was present in traces from both of these variants (in particular, the bipolar par of leads lP and cP). Overall, the amplitude of gamma activity increased with increases in the distance between the electrodes constituting the bipolar pair. This would appear to explain the fact that the amplitude of gamma activity in our

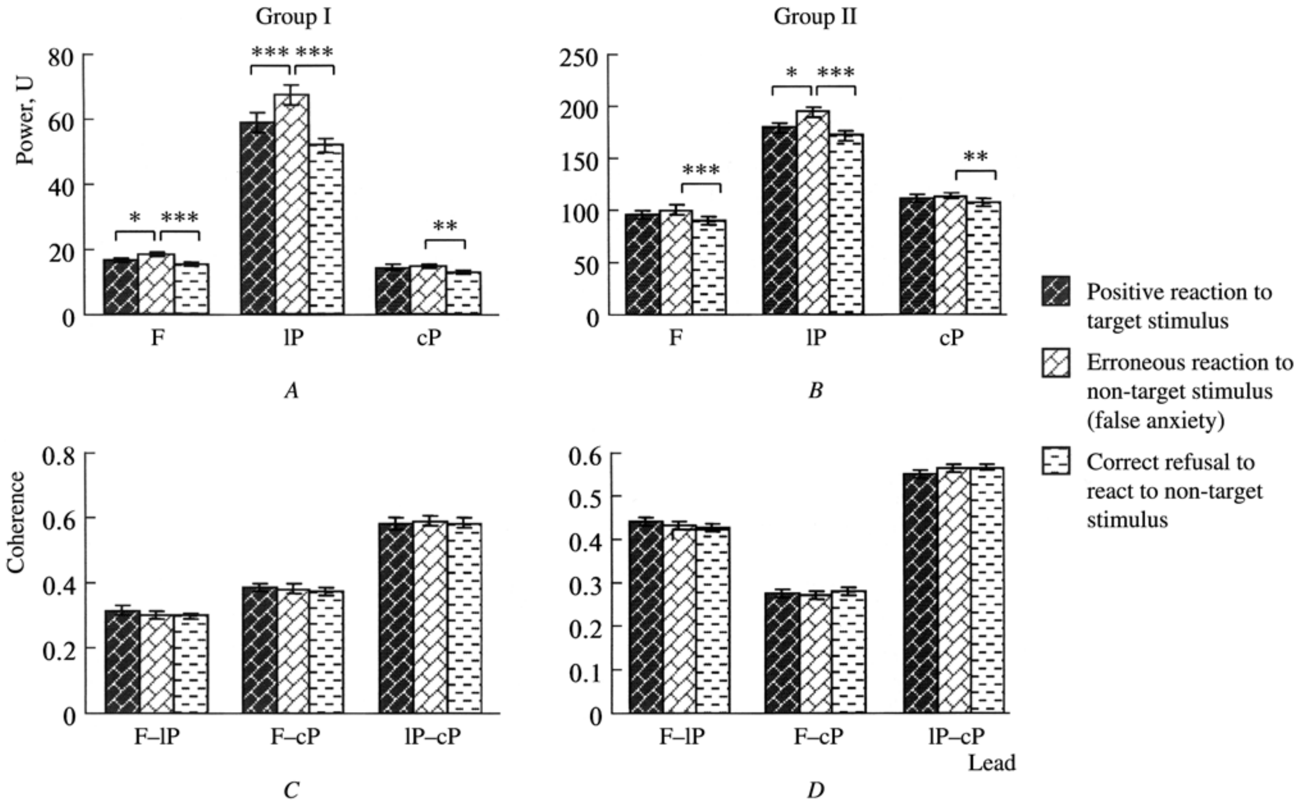

Fig. 3. Background gamma activity before presentation of stimuli with positive operant reactions, erroneous reactions, and correct refusals to react. *A*, *B*) Gamma activity power in groups I ($n = 13$) and II ($n = 27$); *C*, *D*) coherence of gamma activity in groups I ($n = 13$) and II ($n = 27$). For further details see caption to Fig. 1.

experiments was maximal in lead lP (as compared with leads F and cP) – the most distant from the reference electrode. The contribution of myographic activity to the EEG signal recorded could also not be significant, as extensive scalping of the skull was performed during surgery and the distance from the electrodes to the muscles was at least 5–7 mm.

Our studies demonstrated a clear increase in the level of background gamma activity during presentation of sequences of non-target stimuli, which reached a maximum immediately before presentation of a target stimulus, which was followed by a sharp "decay" in the level of spontaneous activity to a lower level. Presumably, during acquisition of the operant reaction in the "active oddball" experimental paradigm, the animals learned that the probability that presentation of one target stimulus would be followed by presentation of another target stimulus was initially low and then increased after a series of several non-target stimuli.

Thus, during some period of time after a target stimulus, there was no subjective need for the animal to discriminate stimuli, such that the level of sustained attention by the animal decreased. Then, as several non-target stimuli followed, when the expected probability that a target stimulus would appear started to increase, there was a corresponding increase in the animal's attention. This effect was also noted in Dumenko's studies: experiments on dogs trained to execute an operant movement showed that both the power and the coherence of the gamma rhythm increased during the interstimulus interval as the conditioned signal was expected; the authors interpreted this as a sign of selective attention [2].

The results obtained by comparing gamma activity in the situation of executing an operant movement with that in which the movement was not executed are interesting. Motor reactions (both positive and erroneous) were executed when the power level of the spontaneous background gamma activity before the moment of stimulus activation was greater than before non-execution of a movement in response to the same stimulus. It can be suggested that the increase in the gamma activity power level in the animals was associated with the increase in the level of sustained attention, which facilitated execution of the reaction. Experiments on humans have also demonstrated that the level of gamma activity during the 10 sec before stimulus presentation allowed the nature of the subsequent reaction to be predicted: an increased level of background gamma rhythm was seen before a correct response to the stimulus, while a missed reaction (non-execution) to the stimulus was preceded by a reduction [22].

As noted above, the overall mean level of background activity before non-target stimuli (including both correct refusals to respond and false anxiety) in our experiments was lower than that before target stimuli. A the same time, erroneous reactions themselves (false anxiety) to non-target stimuli were seen at higher levels of background gamma activity than correct reactions to target stimuli. Extreme increases in the level of spontaneous gamma activity appear to impair the process of decision-taking in response to the non-target stimulus and alters the criteria for decision-taking towards executing a reaction even if erroneous. This can be interpreted as a state of "hyperattention" [29].

Thus, our experiments showed that the background gamma activity level reflects the process of tuning the nervous system to detect and discriminate stimuli. These results are in good agreement with the views of Kotlyar and Timofeeva on the important role of tonic activity in organizing conditioned reflex activity and their results demonstrating a relationship between neuron responses and animals' behavioral responses to a signal and the level of background activation [3].

Our data indicate that fluctuations in background gamma activity can be interpreted as a sign of the sustained (tonic) attention [25] which is currently regarded as the lowest level in the hierarchically organized attention system [7]. Sustained attention is a tonic state created by higher-level cortical associative systems (top-down regulation), activation of this state being mediated by a series of cognitive processes (memory, expectation, motivation, etc.). Current concepts of the organization of this manifestation of attention indicate that the leading role is played by the frontoparietal system [10, 16, 23].

In the context of our data, it is interesting to consider the possible mechanisms of the internal causes of the relationship between fluctuations of gamma activity and attention. The current view is that the parameters of gamma rhythm generation are determined mainly by the ongoing level of cholinergic activation of cortical neural networks [11, 13, 27]. Because of the existence of powerful glutamatergic projections from the prefrontal area of the cortex to the basal magnocellular nucleus of the base of the forebrain (BFN) [19, 30] and the ascending cholinergic projections from the BFN to virtually all areas of the cortex [24, 28], the frontoparietal attention system is able to mediate the cholinergic modulation of various areas of the cortex and convert them to a state of synchronization in the gamma range.

Our previous studies of the activity of BFN neurons during execution of a similar operant reaction by rabbits (twitching of the ear) in response to sound stimuli showed that the background level of BFN neuron activity allows high-probability predictions of the execution/missing of the motor response [8].

We have previously suggested that cholinergic innervation supports the level of cortical activation required to attract attention and creates the conditions needed for processing information about the incoming stimulus [8], the resulting gamma rhythm reflecting the nature of the mechanism whereby the information is processed. The present results are consistent with this suggestion, as the variations in the level of gamma activity seen appear to reflect the pretuning of neural networks to selective stimulus detection [9, 11, 16]. Mathematical modeling of neural networks reported by Bergers et al. demonstrated that synchronization of cortical cells in the gamma range occurring in response to acetylcholine increases network reactions to sensory stimuli and decreases their threshold [11]. This approach allowed the effects of sustained attention to be modeled and contrasted with the responses to two different stimuli. Further verification of the suggestion that cholinergic activation has a role in supporting attention requires direct assessment of the activity of the animal's cholinergic system during execution of the behavioral task used in the study reported here.

In conclusion, it should be noted that according to our results, gamma activity is an appropriate physiological measure of attention in rabbits during execution of the "active oddball" paradigm and this behavioral task used can be used for more detailed neurophysiological study of the cerebral mechanisms generating the gamma rhythm in relation to attention and other cognitive processes.

CONCLUSIONS

1. Background gamma activity reflects the process of tuning the nervous system to recognize stimuli and to react to them. The power and coherence of background gamma activity can be interpreted as neurophysiological indicators of the level of sustained (tonic) attention.
2. Expectation of a target stimulus and its corresponding increase in sustained (tonic) attention are accompanied by increases in the power and coherence of background gamma activity.
3. Appropriate responding to target and non-target stimuli is mediated at a particular level of background gamma activity, which probably corresponds to the optimum level of sustained attention. Decreases in this level lead to missing the motor reaction in response to the target stimulus, while increases, conversely, lead to erroneous reactions to non-target stimuli (false anxiety).

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