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Recognition of direction of uniform and accelerated visual motion and EEG alpha wave phases

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Abstract The perception of visual motion in seven subjects was studied comparing motion towards or away from the fixation point in the left or right hemifield. The light target was moved either at a constant velocity or positively or negatively accelerated to compensate for the magnification factor of the visual cortex. We compared probability and latency of motion recognition when it was asynchronous or synchronized to different phases of the alpha wave of the EEG recorded over the occipital cortex. If the motion accelerated away from the fixation point and was synchronized with the alpha wave it was more likely to be perceived whereas if it was towards the fixation point it was less likely to be detected. However, perception of the constant velocity motion was not changed by locking it to the alpha wave phase. These results support the hypothesis that the scanning waves of excitation spread over the visual cortex periodically and that they are locked to the alpha component of the EEG.

Key words: Human; EEG; Alpha wave; Phase; Recognition; Motion; Uniform; Accelerated; Visual cortex; Magnification factor; Scanning process

1. Introduction

It was suggested [7,19,35] that a wave of excitation, reflected in the EEG alpha wave, spreads over the primary visual cortex every 100 ms. This additional synaptic excitation can increase the firing probability of cortical neurons and thus appears like sequential scanning of the primary visual cortex for the readout of afferent information. The scanning hypothesis concerns the basic cortical operations and the functional significance of neural events participating in the EEG alpha rhythm but has not been proved until recently either directly or in its consequences. Periodical variations of 10 Hz were not found in visual reaction time and in light sensitivity [34]. A burst of alpha activity was demonstrated to influence visual perception negatively [3,4,10,20,32]. On the other hand, subjects exposed to light flashes have seen some patterns that are perhaps due to interference between the scanning mechanisms and the flicker [35]. It must be noted that fast measurement of the alpha wave phase that seems to be necessary for temporally exact stimuli presentation posed technical difficulties; therefore the phase relation of the process remained unknown for many years.

Previously we predicted direct consequences of the original scanning idea [24,27–30]. Let us suppose that the scanning wave spreads from the central to the peripheral part of the visual cortical area [19]. Then recognition of a small figure with a centrally localized contour will be better at relatively earlier phases of the alpha wave while a bigger one will be seen better at relatively later phases. This means that there must be a direct relationship between succession of sizes and of alpha phases by the criterion of recognition probability. The same must be true for alpha phase influence on recognition of motion direction.

Our previous studies tested the consequences of the original hypothesis for recognition of the stationary (flashing) geometrical figures [24–30]. We revealed an inverse relation between figure size and phases of alpha wave. Recognition of small figures was significantly better at relatively later phases of alpha wave, while for bigger ones recognition was better at earlier phases. This data confirmed the scanning hypothesis but suggested that the direction of spread of the alpha wave was opposite to that proposed originally.

It seems reasonable to check the scanning idea under recognition of visual motion [11,12,26,31]. We supposed that it would be possible to observe the effect of synchronizing two waves: alpha wave and the wave evoked by our moving stimulus. Cortical topography is a resultant of a logarithmic transformation of the visual space according to the magnification factor [6,22]. This means that uniform visual motion in visual space will be accelerated in cortical space. This is why we proposed to compare the influence of alpha wave phase on recognition of the uniform and accelerated stimulus motion. In the case of accelerated motion taking into account the magnification factor, we expected to obtain uniform (non-accelerated) spreading of the evoked cortical excitation and thus making possible alpha influence more effective.

2. Methods

2.1. Subjects

Experimental and control sessions (140) involved 7 adult (19–25 years) all right-handed volunteers with normal vision. Subjects' ethical permission was received. We trained subjects during one session to recognize the motion used to eliminate alpha blocking. The subject was instructed to fixate gaze on the fixation point after the sound signal that was given 1–3 s (randomly varied) before stimulation and told to shift one of two handles in response to seeing light motion.

2.2. EEG recording and analysis

Monopolar EEG recordings were made with an active electrode in the right occipital region: the point 3 cm higher and 3 cm to the right of the *inion*; a reference electrode was placed on the left ear. We determined dominant frequency in the alpha range of the EEG power spectrum with the accuracy of 1 Hz. A selective frequency filter with central frequency equal to the peak value in the alpha band extracted alpha activity from EEG. Tuning of the filter allows suppression of the neighbouring frequencies (± 1 Hz from its maximal sensitivity) to the level of 0.15 of the maximal response. The output signal of the filter was fed into a computer through an analogue digital converter (ADC). To avoid too frequent stimuli triggering by low-amplitude

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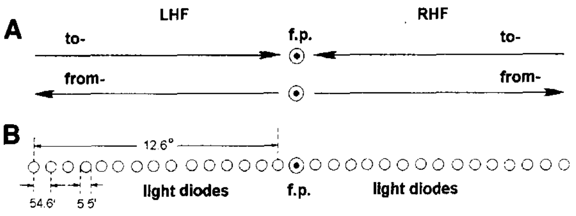

Fig. 1. Scheme of the visual motion presentation. (A) Directions of motion: to fixation point (f.p.) and from f.p. in the left (LHF) and right (RHF) hemifields. (B) Composition of the row of light diodes and its sizes (in angular minutes (′) and degrees (°)).

alpha waves the triggering threshold was fixed at the level of 0.75 of absolute amplitude maximum of the filtered EEG.

2.3. Stimulation

In a light-proof chamber under photopic background illumination (6 cd/m^2) the apparent motion [1] of the light spot was presented into the left or right hemifield and to or from the fixation point (Fig. 1A) in a randomized order. The motion was displayed on a horizontally located row of 30 light diodes (Fig. 1B) with the size of the diode of about 5.5′ (angular minutes) and the distance between their centers of 54.6′. The light power of the diode was of 0.8×10^{-12} Wt/cm^2, the duration of the switching was of 1.9–2.8 ms, the delays between their switching changed in a rather wide range to produce different speeds of motion and/or to change its type (uniform or accelerated). A white fixation point (f.p.) was located in the middle position in the row; 15 diodes were located on the right side from the fixation point and 15 on the left side (Fig. 1B). The length of each light path on 15 diodes was equal to 12.6° (angular degrees), duration of the motion was equal to the individual alpha wave period. We adjusted exposure of each diode in the control conditions individually by a criterion of recognition probability of 0.7–0.9.

The velocity of the uniform motion was typically (for alpha frequency of 10 Hz) equal to 124.9°/s, while the velocity of accelerated motion was changed in the limits of 48–291.2°/s or of 291.2–48°/s depending on its direction to compensate for the cortical magnification factor [6]. For this purpose the speed of motion for both directions was minimal at the central part of the visual field and maximal at its peripheral part. Constant speed of the evoked cortical excitation must be produced in this case because the strongly enlarged cortical projection of fovea travelled with the same speed as the weakly enlarged cortical projection of the visual field periphery.

2.4. Computer control of stimuli presentation

The computer controlled the exact moment of starting the motion. It measured the signal amplitude in the current sample (1 ms) of filtered EEG (in the alpha band) and compared it with the abovementioned amplitude threshold. If the signal exceeded the threshold, the computer looked for 1 of the 4 phases of alpha wave and triggered, in a randomized order with a delay of no more than 1 ms, 1 of the 4 stimulus directions and sides of motion. One from the 4 phases of the EEG alpha wave were used: (1) zero-line crossing on the descending phase, (2) negative peak, (3) zero-line crossing on the ascending phase, and (4) positive peak.

2.5. Controls

In the control the computer presented motions with the same mean rate as in the experiment but independent of the alpha wave phases. The control conditions did not differ from the experimental ones in either the level of the alpha activity or the arrangement of the experimental procedure. Only synchronization of the stimuli with alpha wave was omitted. We never informed our subjects of the experimental or the control nature of the current session. In the special control sessions we exclude eye motions and blinks by the computer control of the horizontal eletrooculogram (EOG).

2.6. Course of experiment and subject's motor responses

The experiment lasted 60–70 min with two intervals for rest; during the session we presented 160 stimuli in 4 directions of motion and at 4 phases of the alpha wave. Thus, for each of the 16 combinations of stimuli and phases we used 10 stimulus presentations. In the force-choice procedure we instructed subjects to shift one of the two handles. (1) The right handle was moved by the right hand to the right side if there was motion of light at the right hemifield directed from the fixation point. (2) The same handle was shifted with the same hand to the left side if the motion at the right side was directed to the fixation point. (3 and 4) The symmetrical situation was observed for the left hemifield with the left hand and the left handle. We also recorded latency of these responses.

2.7. Statistical analysis

After the session the computer plotted the matrix of recognition probability (direction and side of stimuli motion vs. alpha wave phases). We used single and paired t-tests for the comparison of experimental and control data and for defining phase relation.

3. Results

3.1. Recognition of accelerated motion (mean data)

In the control condition a clear and reliable preference for accelerated motions directed to the fixation point (Fig. 2A) was revealed (see also: [2,11–15,17,21,26,31]. We name the motion towards the fovea 'to-direction' to distinguish it from the motion away from the fixation point ('from-direction'). The difference between mean probability of recognition of 'to-' and 'from-direction' was highly significant ($dP = 0.135 \pm 0.046$; $t = 2.93$; $P < 0.01$). We did not find significant differences in recognition of motion direction between the right and the left hemifields (left and right hemisphere, correspondingly), as well as for 'reading' and opposite direction ($P > 0.05$).

Under synchronization of motion with alpha wave phases the preference for the 'to-direction' changed to a preference for the 'from-direction' (Fig. 2B). Motion from the fixation point became better recognized ($P < 0.01$) than the 'to-' one (Fig. 2C). That was the result of relative growth of the recognition probability for the 'from-direction' and its drop for the 'to-direction'.

3.2. Alpha wave phases and recognition of accelerated motion

The changes described above showed dependence on the alpha wave phase. Thus, phases 2 and especially 4 look like the optimum, while phases 1 and 3 produced fewer effects

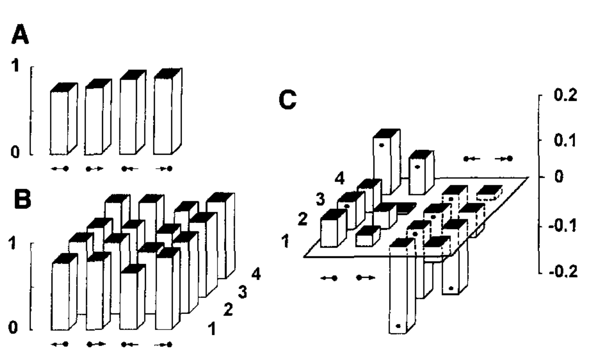

Fig. 2. Dependence of the probability of recognition of accelerated visual motion (ordinate) on its side and direction (shown by symbols: the black spot shows the fixation point) and on EEG alpha-wave phases (1–4) used for synchronization of the motion beginning. (A) control; (B) synchronization of motion beginning with alpha-wave phases; (C) difference between the experiment (B) and the control (A). Recognition improvement is shown as an upward deflection, its worsening — as a downward one. The mean data for seven observers, the black spot marks significant differences ($P < 0.05$).

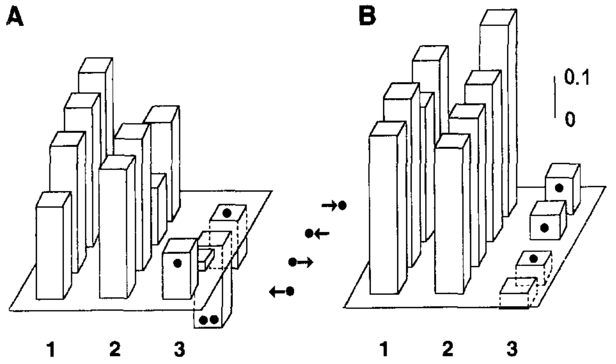

Fig. 3. Probability of the recognition (vertical axes) of direction and side of accelerated visual motion (symbols as in Fig. 2) in two groups of observers (A,B) in control (1), in experiment (2), and the difference between them (3). The mean data for 5 (A) and 2 subjects (B); one black dot corresponds to $P < 0.05$, two black dots to $P < 0.01$.

(Fig. 2C, 'from-directions'). The drop of the recognition probability for the 'to-direction' showed clear preference for phase 1 in the right hemifield and for phase 2 at the left side (Fig. 2C, 'to-directions'). Fig. 2C shows a clear tendency for decrease of recognition of the 'to-direction' synchronized with relatively earlier alpha wave phases (1 and 2) and improvement of recognition of the 'from-direction' synchronized with later phase 4. We would also like to mention that the right hemisphere (left hemifield) showed clearer phase dependence.

3.3. Recognition of accelerated motion in two groups of subjects

The above-mentioned difference between experiment and control manifests itself not only in the mean data, but was typical for five out of seven of our observers (Fig. 3A). In the second group (two observers) the recognition level changed in the experiment contrary to the mean results and with the first group (Fig. 3B). Recognition of the 'to-direction' in the experiment improved, while the 'from-direction' reduced. Control directional preference in these groups of subjects also differs (Fig. 3): the second group shows no preference for the 'to-direction'.

3.4. Recognition of uniform motion

Less influence of alpha wave on the recognition of uniform motion in comparison with accelerated motion was revealed (Fig. 4). The mean data for all seven subjects (Fig. 4A) showed an absence of any reliable changes of recognition of all motion directions in the experiment in comparison with the control. The same is illustrated (Fig. 4B) for one of our subjects: significant lowering of recognition probability in the experiment (Fig. 4E) with accelerated to-motion (Fig. 4B, 3 and 4) which disappears for all directions of the uniform motion (Fig. 4C).

3.5. Eye movements and directional perception

To control the influence of possible eye movements on recognition of the light motion direction, the computer excludes the responses that coincided with eye movements and with blinks, recorded by horizontal EOG. It appears that in our study the eye movements produced no reliable influence on the level of recognition both in the control and in the experiment ($P > 0.05$).

3.6. Latency of recognition of motion direction

The response latencies to the accelerated motion in the control were reliably ($P < 0.05$) shorter (mean of 28%) for 'from-' than for 'to-directions' in both hemifields (Fig. 5, compare A with C and B with D). In the experiment, latency becomes reliably ($P < 0.001$) longer (mean change of +20%) especially for 'to-directions'. The response latency to the uniform motion became longer than for the accelerated one in the control on 14%, in the experiment on 5% and, in the experiment in comparison with the control, only 9% ($P > 0.05$). Small and unreliable differences exist between mean latency of the responses for 'to-' and for 'from-direction' of the uniform motion and between control and experimental conditions.

4. Discussion

4.1. Confirmation of the Pitts and McCulloch hypothesis

In the present study we tested the scanning hypothesis in the context of recognition of the direction of motion. We

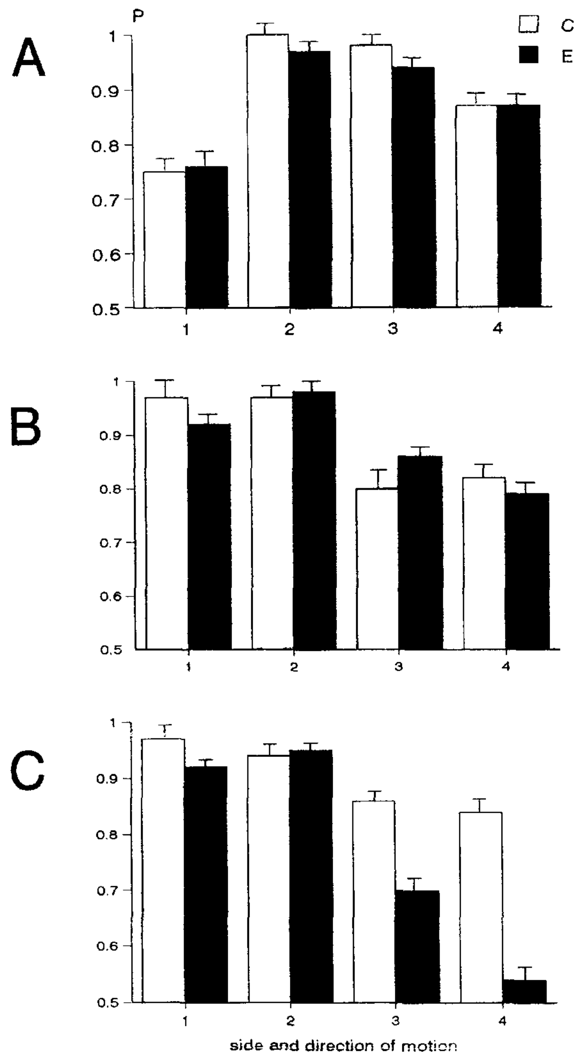

Fig. 4. (A) Probability of the recognition (ordinate) of direction and side of uniform motion in the control (C) and in the experimental (E) in seven observers. (B,C) Recognition of uniform (B) and accelerated motion (C) by observer V.L. 1 and 2, motions directed from the fixation point; 3 and 4, motions directed to the fixation point; 1 and 3, motions in the left hemifield; 2 and 4, in the right hemifield. Mean data and their errors (S.E.M.).

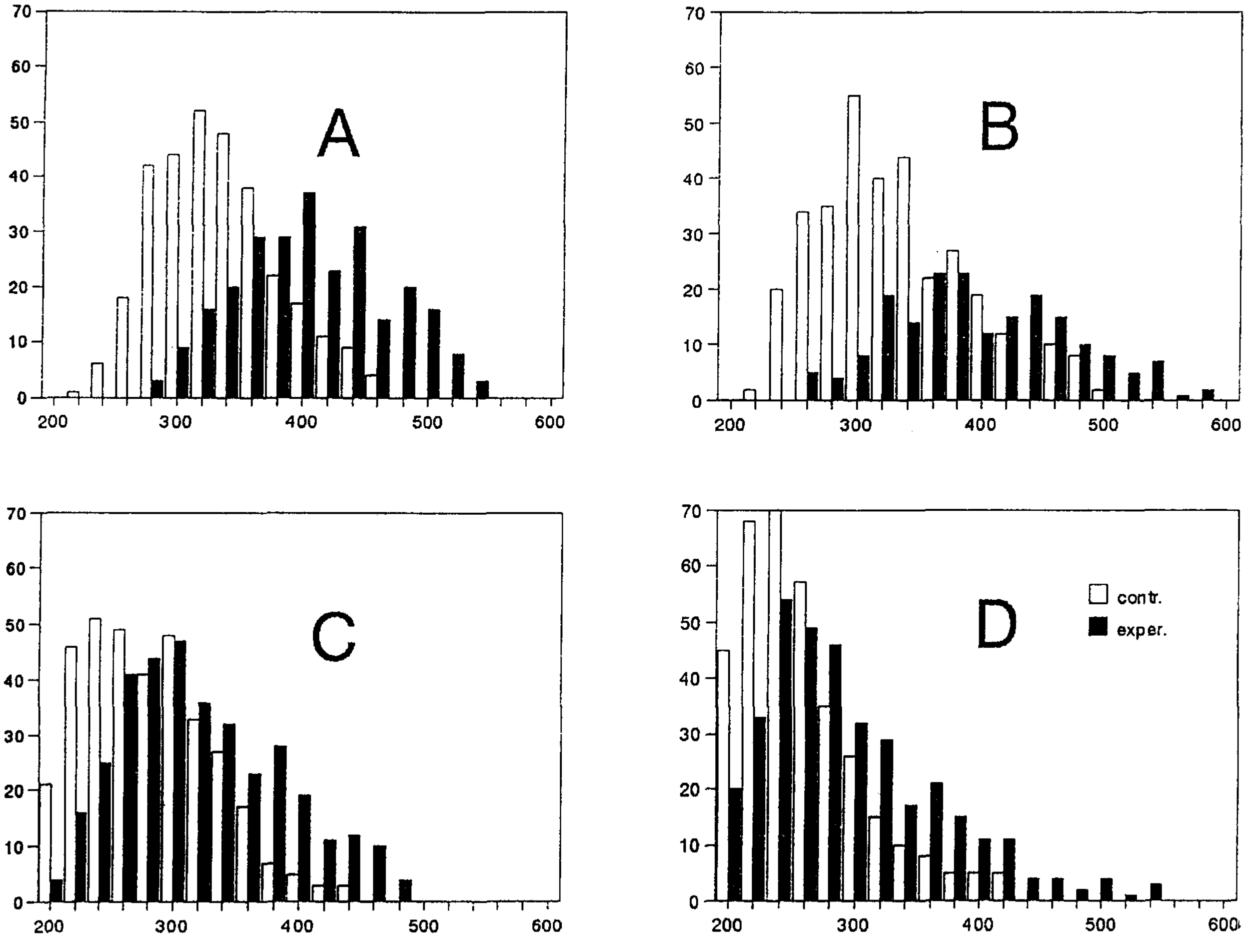

Fig. 5. Distribution of the motor response latencies (abscissa, ms) for the recognition of accelerated motion by observer V.L. (A,B) Directions to the fixation point; (C,D) directions from the fixation point; (A,C) left hemifield; (B,D) right hemifield. White bars, control; black bars, experimental (all alpha-wave phases together). Ordinate, number of the responses.

presume that this recognition will change if we synchronize or let go towards two excitatory waves in the visual cortex: alpha wave and the wave evoked by the moving stimulus. We also planned to compare the alpha effect on recognition of uniform and accelerated stimulus motion. In accelerated motion [31] as a result of the magnification factor [6], we postulated uniform (non-accelerated) spreading of the evoked cortical excitation thus making possible alpha influence more effective.

We found reliable changes in the recognition probability and latency under synchronization of the accelerated motion with that of phases of the alpha wave. Perception of the motion directed away from the fixation point improves in comparison with the control, while perception of motion in the opposite direction typically decreases. Uniform motion fails to produce these effects. Thus, the present data supports our main presumptions.

4.2. Characteristics of the scanning wave in the visual cortex

Our previous study showed [24,27–30] that the wave of excitation which is locked to the alpha component of EEG appears in the cortical projection of the near periphery of the visual field (9–12° from gaze). The wave travels to the cortical representation of the fovea and reaches it during the alpha wave period. Our present data allows us to detail the characteristics of the spreading wave. A reliable effect of the alpha wave on recognition probability and latency for accelerated motion and absence of the effect for uniform motion was revealed. This proves the assumption of a uniform alpha wave spreading over the cortex. Actually, only uniform spread of the evoked cortical excitation under accelerated stimulus motion allows the synchronization not only of the initial moment of two waves' movements, but for receiving their full overlap and thus to reveal the maximal possible effect. It must be remembered that in our previous study a linear link between the stimulus size and alpha wave phase was demonstrated if the figure size (equivalent of the cortical space) was plotted logarithmically according to the magnification factor [6]. All of this means that spreading of alpha wave over the visual cortex is practically uniform.

4.3. Direction of the scanning wave spreading and recognition of light motion direction

It is difficult to provide a sound explanation for directional preference (from the fixation point) revealed in our experiment. Explanation of the effect may be found in different mechanisms of stationary and moving stimulus perception [16,18,33]. Units with orientation selectivity play the main role in the early cortical stage of configuration recognition [16]. However, the perception of motion direction is based on activity of directional tuned cortical units (see reviews: [1,5,9,23]) with high sensitivity to the spatio-temporal gradient of the afferent signal. This gradient must be greatest in the case of opposite (oncoming) direction of movement of two excitatory cortical waves: the alpha wave and the one evoked by light. Directional selective cortical units with receptive fields located at the near periphery of the visual field prefer mostly high speed of visual motion [18] that is equivalent to a high gradient of the excitation.

We cannot yet explain the data we have found in two of our seven subjects with opposite changes of recognition in the experiment. One or two subjects with non-typical direction of the process in our recent and previous experiments indicate individual characteristics and two possible opposite directions of the scanning wave propagation.

4.4. Masking of the revealed effect

Some factors could mask the tested phenomenon but they failed to do that in our experiment. This additionally proved the non-accidental nature of these results. Most substantial of the factors is a phase shift between filtered and non-filtered EEG [30]. This will result in some error of the 'true' phase estimation due to delay introduced by the analog filter. We would like to stress that the phase shift is equal for all phases of the alpha wave and that, to some extent, it is not of great importance for our conclusions. It is the succession of the phases rather than the exact phase values themselves that is of significance for our conclusions. That is why we discuss 'later' or 'earlier' phases, but cannot assert their angle value purely quantitatively. In this 'distorted' situation the statistically significant differences which we observed in the perception of stimulus motion presented at different phases of the alpha wave, support the described phenomenon.

4.5. Possible functional meaning of the spreading alpha wave

Functional meaning of the periodically moving alpha process in the visual cortex was postulated [19]. Authors believed that it: (1) ensured an invariant visual recognition of size, rotation and retinal localization of the recognized figures; (2) reduced the volume of the information channel between area 17 and other visual fields and consents this volume with reality; and (3) ensured a productive spatio-temporal [8] information presentation at the output of the visual cortex instead of a purely spatial one. It is difficult to add something new to these advanced speculations and to discuss them in detail. It must only be noted that these functions are an important addition to the widely spread ideas on the timing function of alpha activity [32].

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