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Visual illusions and travelling alpha waves produced by flicker at alpha frequency

I.A. Shevelev*, V.M. Kamenkovich, E.D. Bark, V.M. Verkhlutov, G.A. Sharaev, E.S. Mikhailova

Department of Sensory Physiology, Institute of Higher Nervous Activity and Neurophysiology, Russian Academy of Sciences, Moscow 117865, Russia

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Abstract

The aim of the study was to obtain some experimental evidence of the 'scanning hypothesis' that links electroencephalogram (EEG) alpha-activity with rhythmically spreading waves in the visual cortex. The hypothesis was tested in experiments with 29 healthy adults. Under flicker stimulation through closed lids with the frequency of the individual alpha-rhythm, all subjects perceived illusory visual objects (a ring or a circle, a spiral or a spiral spring, or a grid). Most frequently noted was the perception of a ring or a circle; less frequently, a three-dimensional spiral; and even less frequently, a curved grid. It was found that the optimal stimulation frequency for this effect was tightly connected with the dominant alpha-rhythm frequency, with a correlation coefficient of 0.86. The probability of observing the ring and spiral illusion was highest at this frequency, while that for the grid illusion occurred at frequencies that differed by ± 1–2 Hz. We observed 10 typical trajectories of travelling EEG alpha-waves on the scalp, and a significant interrelation between the occipital–frontal trajectory and illusions of the ring and spiral. The link between these effects and the propagation of the wave process through the visual cortex, as reflected by the EEG alpha-rhythm, is discussed. The data support the hypothesis of (Pitts, W. McCulloch, W.S., 1947), which proposes the scanning of the visual cortex by a spreading wave process operating at the frequency of the alpha-rhythm, which reads information from the visual cortex. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Visual illusion; Alpha rhythm; Scanning process; Electroencephalogram; Travelling wave; Flicker

* Corresponding author. Tel.: + 7-095-334-4281; fax: + 7-095-338-8500.

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1. Introduction

The functional importance of alpha-activity in the visual cortex is as yet unclear (Pitts and McCulloch, 1947; Walter, 1953; Dubikaitis and Dubikaitis, 1962; Remond, 1968; Dubikaitis, 1975; Plotkin, 1976; Guselnikov and Iznak, 1983; Markand, 1990; Sheppard and Boyer, 1990; Lopes da Silva, 1991; Barlow, 1993; Hughes, 1995; Niedermeyer, 1997). It has been suggested that the alpha-rhythm represents the activity of a cortical scanning mechanism which sequentially examines parts of the visual field (Pitts and McCulloch 1947; Walter 1953). According to this hypothesis, every 100 ms the wave of excitation, which is reflected by the EEG alpha-wave arising in the cortical projection of the center of the visual field, spreads over the primary visual cortex. The ring-shaped wave starts to spread outwards, and reaches the edges of area 17 after 100 ms. This excitation summates the visually evoked PSPs of neurons, facilitating their firing. Thus, this additional synaptic excitation is supposed to successively increase the firing probability of neighboring groups of cortical neurons, and appears to scan the visual cortex for the sequential transmission of afferent information to other cortical areas. Despite the fact that this interesting idea has direct relevance to the cortical processing and to the functional meaning of the neuronal events involved in generation the EEG alpha-rhythms, it has not yet been subjected to strict verification either directly or in terms of its consequences.

For a long time the scanning idea did not receive much experimental support. Some studies failed to observe alpha-rhythm synchronous cyclic oscillations in light sensitivity and response time (Walsh, 1952), as well as any stroboscopic perceptual effects under stimulation with flashed patterns (Mackay, 1953). According to some observations (Bechtereva and Zontov, 1962; Varela et al., 1981; Bohdanecky et al., 1983; Radill et al., 1984; Iznak, 1989, 1990) a burst of alpha-activity negatively influences visual perception. On the other hand, individual patterns seen by subjects exposed to flashes have been plausibly ascribed to the interference between them and the scanning mechanism (Walter, 1953). However, the extremely fast measurement of the alpha-wave phase that seems to be necessary for exact stimulation timing was technically difficult for many years.

To test the scanning hypothesis, we analyzed a direct consequence of it in controlled psychophysical experiments (Shevelev et al., 1985, 1988, 1991a; Shevelev, 1988, 1995). Let us suppose that the scanning wave spreads from the central to the peripheral parts of the visual cortex. In this case, the recognition of small figures would be better at relatively earlier phases of the alpha-wave recorded at a certain site on the scalp, while that of bigger ones at relatively later phases. In previous studies, we tested this consequence for the recognition of flashing geometrical figures (Shevelev et al., 1985, 1988, 1991a; Shevelev, 1988, 1995, 1997), as well as for the recognition of direction of visual motion (Shevelev et al., 1991b, 1996b; Kamenkovich and Shevelev, 1994; Kamenkovich et al., 1995; Shevelev, 1995, 1997). It was shown that the recognition improved significantly when small figures were presented at relatively late phases of the alpha-wave and when large figures (up to 9°) were presented at relatively early phases (Shevelev, 1988, 1995, 1997; Shevelev et al., 1988, 1991a). These studies provided indirect evidence of the scanning hypothesis. At the same time, they indicated a periphery–center direction of the wave motion. Besides, in our early experiments with non-patterned visual stimulation with alpha-frequency through closed lids, our subjects perceived patterned visual illusions (a circle, a spiral or a grid) that appeared at a frequency equal to the individual alpha-frequency (Shevelev et al., 1996a; Kamenkovich et al., 1997; Shevelev, 1997).

The aim of the present study was to find some additional evidence of the 'scanning hypothesis'. Under a flicker stimulation with alpha-frequency, we expected to reveal an illusory visual perception of the spreading cortical wave. It was of special interest to study the possible interrelation between these illusions and so called 'travelling' alpha-waves (Goldman et al., 1949; Livanov and Ananyev, 1955; Monakhov, 1961; Lehmann, 1971; Suzuki, 1974; Dubikaitis, 1975; Knipst et al., 1982;