Visual deviant stimuli produce mismatch responses in the amplitude dynamics of neuronal oscillations

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ABSTRACT

Objectives: Auditory and visual deviant stimuli evoke mismatch negativity (MMN) responses, which can be recorded with electroencephalography (EEG) and magnetoencephalography (MEG). However, little is known about the role of neuronal oscillations in encoding of rare stimuli. We aimed at verifying the existence of a mechanism for the detection of deviant visual stimuli on the basis of oscillatory responses, so-called visual mismatch oscillatory response (vMOR).
Methods: Peripheral visual stimuli in an oddball paradigm, standard vs. deviant (7:1), were presented to twenty healthy subjects. The oscillatory responses to an infrequent change in the direction of moving peripheral stimuli were recorded with a 60-channel EEG system. In order to enhance the detection of oscillatory responses, we used the common spatial pattern (CSP) algorithm, designed for the optimal extraction of changes in the amplitude of oscillations.
Results: Both standard and deviant visual stimuli produced Event-Related Desynchronization (ERD) and Synchronization (ERS) primarily in the occipito–parietal cortical areas. ERD and ERS had overlapping time-courses and peaked at about 500–730 ms. These oscillatory responses, however, were significantly stronger for the deviant than for the standard stimuli. A difference between the oscillatory responses to deviant and standard stimuli thus reflects the presence of vMOR.
Conclusions: The present study shows that the detection of visual deviant stimuli can be reflected in both synchronization and desynchronization of neuronal oscillations. This broadens our knowledge about the brain mechanisms encoding deviant sensory stimuli.

Introduction

Rare deviant stimuli are biologically important, as they usually indicate, in an otherwise predictable environment, a change that can lead to behaviorally relevant consequences (Sokolov et al., 2002). In the human brain, such changes in stimulus properties can be detected electrophysiologically via recording of

evoked responses. The auditory mismatch negativity (MMN) is a classic example of deviant stimulus detection (for reviews, see Näätänen et al., 2011, 2007). Analogously, MMN to visual stimuli can also be recorded (visual mismatch negativity, vMMN); it is a negative event-related potential with a posterior/occipito–parietal scalp distribution peaking at around 150–400 ms after the onset of deviant visual stimuli (Kimura, 2012). The vMMN can be elicited with an oddball paradigm, where infrequent stimuli are semi-randomly embedded among frequent standard stimuli (Kimura, 2012; Pazo-Alvarez et al., 2003; Stefanics et al., 2012, 2014). vMMN is sensitive to deviant stimulus characteristics such as changes in contrast, color, shape, movement direction, form, orientation, or spatial frequency (Czigler, 2014; Kimura, 2012; Pazo-Alvarez et al., 2003; Stefanics et al., 2012).

Although traditional evoked mismatch responses have been found in auditory and visual modalities, it is less clear whether deviant stimuli can in addition produce changes in the amplitude

dynamics of auditory (Fuentemilla et al., 2008; Hsiao et al., 2009; Ko et al., 2012) or visual neuronal oscillations (Stothart and Kazanina, 2013). As evoked responses and neuronal oscillations represent two major modes of brain functioning (Roach and Mathalon, 2008), answering this question is important for understanding neuronal processing responsible for change detection.

It would be particularly important to show whether alpha oscillations can produce mismatch responses to deviant stimuli. This is because the alpha rhythm has been shown to reflect inhibitory processes in the cortex; thus, a change in its amplitude would relate to patterns of excitation/inhibition caused by the deviant stimuli. An increase in the amplitude of oscillations (also referred to as event-related synchronization, ERS (Pfurtscheller and Lopes da Silva, 1999)) indicates the presence of task-related inhibitory activity in a given area (Jensen et al., 2014; Jensen and Mazaheri, 2010; Palva and Palva, 2007), while an attenuation of oscillatory amplitude (also referred to as event-related desynchronization, ERD) indicates an underlying active process, characterized by increased excitation (Pfurtscheller and Lopes da Silva, 1999; Sauseng et al., 2005; Thut et al., 2012).

In the present study, we addressed the question of whether the changes in the strength of alpha-rhythm ERD/ERS can reflect a neuronal response to deviant stimuli and whether in fact both desynchronization and synchronization can occur simultaneously. Given that we studied responses to visual stimuli, we refer below to the changes in the oscillations to deviant stimuli as visual mismatch oscillatory responses (vMOR).

An important factor to be considered is the multitude of oscillatory processes in the alpha frequency range, which are heavily superposed on the sensor level in EEG or MEG (Haufe et al., 2014). In order to enhance the detection of oscillatory responses to deviant stimuli, we used an optimization algorithm (common spatial patterns, CSP; Blankertz et al., 2008) for the efficient extraction of oscillatory components.

Method

Subjects

Twenty healthy volunteers (11 females, 9 males; 28 ± 3 years; 1 left-handed and 19 right-handed) with normal or corrected-to-normal vision were enrolled. None of the subjects had neurological diseases. The experimental protocol was approved by the Ethics Committee of Helsinki University Hospital and was in compliance with the Declaration of Helsinki. The subjects gave their written informed consent prior to the experiments.

Stimuli

Peripheral vision is important since it allows detection of unexpected or deviant signals and in many cases our survival depends on the ability to perceive the movement of significant objects (e.g., detecting peripheral driving vehicles on the road, avoiding a predator or a falling tree, etc.). Therefore, it is important to describe the neuronal mechanisms of such stimulation. Consequently, in this study, we use two displays to simulate a more realistic situation.

The subjects sat in a comfortable chair and were instructed to remain awake, to keep their eyes open and to focus on a white fixation cross presented on a black background in front of them. They were also advised to minimize any unnecessary movements and blinking. Two 21-inch full-HD screens were placed laterally at 80 cm from the medial head line. The viewing angles of each monitor ranged from 59° (distal side) to 90° (proximal side) (Fig. 1A).

White circular spots (radius of 150 pixels, 37 mm, visual angle 2.65°) were presented simultaneously on both screens (one spot per screen). The spots moved in a circle with angular velocity of about 42 rpm, the direction of this rotary motion defining the
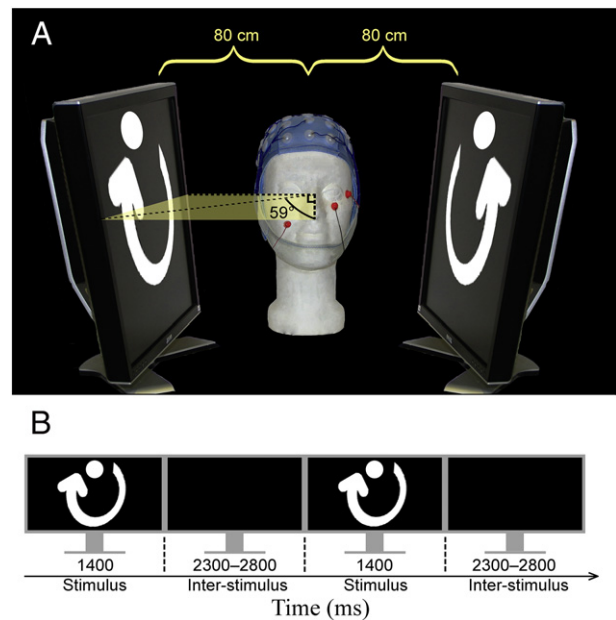

Fig. 1. Experimental setup and stimulus paradigm. A) Two screens were placed laterally at 80 cm from the medial head line. B) The stimulus duration was 1400 ms; the inter-stimulus interval varied randomly between 2300 and 2800 ms.

difference between the standard and deviant stimuli. The direction of the motion was randomized among subjects. From 657 to 837 (800 ± 8) stimuli were presented semi-randomly in an odd-ball paradigm with a 1:7 ratio, i.e., 81 to 100 (98 ± 1) deviants and 576 to 737 (702 ± 8) standards. The stimulus duration was 1400 ms which corresponds to one rotation of the spots. The inter-stimulus interval was randomized between 2300 and 2800 ms (Fig. 1B).

EEG recordings

The electric potentials on the scalp were recorded with a 60-channel eXimia EEG (Nexstim Plc., Helsinki, Finland), electrodes being placed according to the international 10–20 system. The signals were referenced to the right mastoid; the ground electrode was over the right cheek bone. Eye movements were recorded with two additional electrodes; one electrooculography (EOG) electrode was placed on the frontal process of the zygomatic bone and the other under the eye (Fig. 1A). The impedance of all electrodes was kept below 5 kΩ. The signals were band-pass filtered from 0.1 to 350 Hz and digitized at 1450 Hz. The EEG was recorded for about 90 min with a 1-minute break after every 5 min of recording.

Electrooculography

The individual EOGs were processed with band-pass (0.5–40 Hz) and notch filters (48–52 Hz) to remove high-frequency and the remaining power-line interference, respectively. Both filters were fourth-order, Butterworth, and zero-phase. The data of eighteen individual EOGs were averaged for standard and deviant stimuli; data of two subjects were excluded due to poor EOG quality (i.e., excessive noise and artifacts).

Data analysis

Offline analysis was performed with Matlab (The Mathworks, Inc., Natick, Massachusetts, USA). The EEG recordings were visually inspected. The epochs with amplitudes larger than $\pm 100\,\mu V$ or