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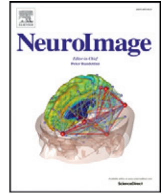

Early visual cortical responses produced by checkerboard pattern stimulation

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ABSTRACT

Visual evoked potentials have been traditionally triggered with flash or reversing checkerboard stimuli and recorded with electroencephalographic techniques, largely but not exclusively in clinical or clinically related settings. They have been crucial in determining the healthy functioning or otherwise of the visual pathways up to and including the cerebral cortex. They have typically given early response latencies of 100 ms, the source of which has been attributed to V1, with the prestriate cortex being secondarily activated somewhat later. On the other hand, magnetoencephalographic studies using stimuli better tailored to the physiology of individual, specialized, visual areas have given early latencies of <50 ms with the sources localized in both striate (V1) and prestriate cortex. In this study, we used the reversing checkerboard pattern as a stimulus and recorded cortical visual evoked magnetic fields with magnetoencephalography, to establish whether very early responses can be traced to (estimated) in both striate and prestriate cortex, since such a demonstration would enhance considerably the power of this classical approach in clinical investigations. Our results show that cortical responses evoked by checkerboard patterns can be detected before 50 ms post-stimulus onset and that their sources can be estimated in both striate and prestriate cortex, suggesting a strong parallel input from the sub-cortex to both striate and prestriate divisions of the visual cortex.

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1. Introduction

Visual evoked potentials (VEPs) and visual evoked magnetic fields (VEFs) have played a leading role in clinical settings, primarily to establish whether the visual pathways up to, and including, the visual cortex, are functioning normally (Nakasato and Yoshimoto, 2000; Tobimatsu and Celesia, 2006). The technique of choice for recording them has been electroencephalography (EEG) and the results obtained have also been used in more theoretical considerations about how the visual brain functions (Barnikol et al., 2006; Hatanaka et al., 1997; Kaneoke et al., 2005; Luck, 2005; Tobimatsu and Celesia, 2006). Since their discovery (Adrian and Mattews, 1934; Cobb and Dawson, 1960; Monnier, 1949; Spehlmann, 1965), it has been generally supposed that the initial stage of visual processing in cortex starts at around 100 ms after stimulus onset, although earlier latencies, in the 60–80 ms range have been given (Clark et al., 1995; Jeffreys and Axford, 1972a,b). The source of the earliest component of VEPs/VEFs has been usually estimated to be in V1 (Reviewed in Di Russo et al., 2002; Luck, 2005).

This general picture is the result of using flash stimuli or of reversing checkerboard patterns, neither of which is specifically tailored to the physiology of the specialized visual areas. Their main use, instead, has been to test whether the optic nerve and the visual brain are functioning normally as a whole, with little effort made to study the separate systems that constitute the visual brain. Whatever the precise use to which VEP/VEF studies were put, the general consensus that has emerged, of an activation of V1 before the rest of the visual brain, ties in neatly with the hierarchical processing model (Kaneoke et al., 2005; Tobimatsu and Celesia, 2006) which supposes that V1 is the first cortical stage in processing visual signals and is the unique source for building different visual attributes, among them colour and forms of higher complexity, including faces, houses and objects. Nor is this view derived from VEP/VEF studies alone. A similar strong adherence to the serial, hierarchical, doctrine also permeates the literature derived from anatomical and physiological studies (for a recent review, see Wilson and Wilkinson, 2015).

The theoretical limit of the shortest latency which can be recorded from the visual cortex is about 20–30 ms (ffytche et al., 1995); the imaging of temporal activity, using EEG and MEG, in response to stimuli better tailored to the specialized physiology of visual areas, and in particular visual motion, shows that visual signals reach the cortex at latencies of less than 30 ms after stimulus onset (ffytche et al., 1995; Gaglianese et al., 2012). But the earliest responses in this instance are not from V1 but rather from the area specialized for visual motion, namely V5. Nor is this early arrival of signals in the cortex restricted to the motion system. The colour system may also deliver signals to V4 before or at the same time as to V1 while the form system delivers signals to V1 and the relevant prestriate visual areas within the same early time

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frame of 25–45 ms (Shigihara and Zeki, 2013, 2014; Shigihara et al., submitted for publication).

We wanted to use reversing checkerboard patterns to learn whether, in light of our recent results, responses can also be detected at short latencies from both striate and prestriate cortex (Shigihara and Zeki, 2013, 2014; Shigihara et al., submitted for publication). Checkerboard stimuli contain lines and should therefore at least stimulate orientation selective cells and form specific prestriate cortical areas effectively. This seemed an interesting and important question not only in the clinical context but also theoretically. If early responses can be detected with such patterns, then checkerboard patterns can have potentially a more widespread clinical use since they would extend the time range over which the healthy functioning of the visual brain can be ascertained. Theoretically, such a demonstration would also supplement our earlier demonstration of a dual input to the prestriate visual areas, one activating it through V1 and another activating it directly from the lateral geniculate nucleus (LGN) and pulvinar, and thus by-passing V1. This amounts to showing that the parallel processing strategy is used even before V1, in the sense that signals can be recorded from V1 and from prestriate visual areas either simultaneously or in a reverse hierarchy, with the prestriate visual areas being responsive before V1 (ffytche et al., 1995). In brief, in this study we analysed the VEFs produced by a popular and extensively used visual stimulus, namely the reversing "checkerboard pattern" to learn whether, using it, one can also obtain early responses from prestriate visual cortex.

2. Material and methods

2.1. Participants and study design

Twenty healthy adult volunteers (8 female, 1 left-handed, mean age 28.4 ± 5.9 years) took part. None had a history of neurological or psychiatric disorder; written informed consent was obtained from all and the study, which conforms to Code of Ethics of the World Medical Association (Declaration of Helsinki; printed in the British Medical Journal 18 July 1964), was approved by the Ethics Committee of University College London.

2.2. Stimuli and task

Participants sat in a chair inside a magnetically shielded room and viewed a screen 60 cm in front of them. A reversing white and black checkerboard pattern was used as a stimulus and was back-projected by a projector (RM-MSX21G, Victor Company of Japan, Kanagawa, Japan) onto the lower left quadrant of the screen, with a resolution of 800 × 600 pixels at 60 Hz; the whole pattern subtended a visual angle of 9.0° × 9.0° (0.5° × 18 checkerboard patterns) and its centre was located 8.5° to the left and 8.5° below the centre of the screen (Fig. 1). The average luminance of the entire pattern was 8.73 cd/m^2 and the contrast between its squares was 96%. We restricted ourselves to lower (left) quadrant stimulation, for two reasons: (a) to avoid cancellation effects that can occur when both banks of the calcarine sulcus are stimulated (Portin et al., 1999) and (b) because lower quadrant stimulation produces stronger VEFs than upper field stimulation (Portin et al., 1999). The check pattern reversed randomly every 1300–1500 ms. Stimuli were generated and controlled using Cogent 2000 and Cogent Graphics (http://www.vislab.ucl.ac.uk/cogent.php) toolboxes running in MATLAB (MathWorks, Na-tick, MA, USA). The experiment consisted of 4 sessions of 160 stimuli each. Participants fixated a 1.0° diameter fixation point located at the centre of the screen, throughout the runs.

2.3. Scanning details for MEG

Neural responses produced by stimulation were recorded continuously using a 275-channel CTF Omega whole-head gradiometer (VSM MedTech, Coquitlam, Canada). Data were sampled at 1200 Hz with a 200 Hz hardware low-pass filter. Participants were fitted with localizer coils at the nasion and 1 cm anterior to the left and right traguses to monitor head movements during the recording sessions and coregister the MEG data onto individual MRI structural images acquired in a 3 T MRI scanner (Siemens Magnetron Allegra MRI scanner or Trio Tim 3 T scanner, Siemens, Erlangen, Germany). We could not obtain structural scans for 8 of the 20 participants, for a variety of reasons (tattoos, claustrophobia, etc). For these 8 participants, we coregistered the MEG data onto a canonical brain. Trigger signals were recorded for the MEG system through an IEEE 1284 connection. The delay between the trigger signal and the projection of stimuli (33 ms) was confirmed using a photodiode on the screen before scanning participants and was corrected during data processing. Gaze position and blinking were monitored by an EyeLink 1000 eye-tracker (SR Research Ltd., Ontario, Canada).

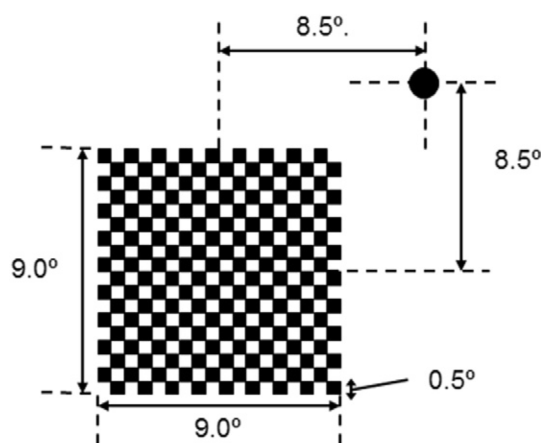

Fig. 1. Diagrammatic representation of the checkerboard pattern and its projection onto the field of view. The fixation point (1.0° in diameter) is located at the centre of the screen. The overall size of the checkerboard pattern was 9.0° × 9.0° and it was projected onto the lower left quadrant, its centre located 8.5° below and to the left of the fixation point. Each side of the pattern extended 0.5 × 0.5°.

2.4. MEG data processing

Data were analysed offline using SPM-12 (http://www.fil.ion.ucl.ac.uk/spm/). They were divided into 1000 ms epochs, each starting 500 ms before stimulus onset. Epochs affected by blink artefacts (detected using the eye-tracker and also by manual inspection of the raw signal data) were discarded and the remaining ones averaged in each run and baseline corrected. 474.3 ± 68.3 responses were recorded for each participant.

2.5. Outline of MEG analysis

MEG analysis consisted of four steps: sensor-level analysis, contour map analysis, source-level analysis, and self-replication test. The sensor-level analysis was used to confirm that MEG detected a VEF before 50 ms post stimulus onset, to confirm that the response amplitude was significantly higher than the baseline level and to identify its latency; contour map analysis was used to confirm that the VEF signals originated from occipital cortex, while the source-level analysis was used to determine which cortical areas were responsible for producing the VEF. The self-replication test was performed at the end of the analysis to improve the reliability of our results.

2.5.1. Sensor-level analysis

From among the 37 occipital sensors based on the sensor names MLO 11–53 and MRO 11–53 defined by SPM-12, we chose the sensor of interest (SOI) which showed the largest root-mean-square (RMS) amplitude of VEF between 25 and 50 ms (SOI approach; Liu et al.,

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