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Spatiotemporal profiles of visual processing with and without primary visual cortex

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ABSTRACT

The spatiotemporal profiles of visual processing are normally distributed in two temporal phases, each lasting about 100 ms. Within each phase, cortical processing begins in V1 and traverses the visual cortical hierarchy. However, the causal role of V1 in starting each of these two phases is unknown. Here we used magnetoencephalography to study the spatiotemporal profiles of visual processing and the causal contribution of V1 in three neurologically intact participants and in a rare patient (GY) with unilateral destruction of V1, in whom residual visual functions mediated by the extra-geniculostriate pathways have been reported. In healthy subjects, visual processing in the first 200 ms post-stimulus onset proceeded in the two usual phases. Normally perceived stimuli in the left hemifield of GY elicited a spatiotemporal profile in the intact right hemisphere that closely matched that of healthy subjects. However, stimuli presented in the cortically blind hemifield produced no detectable response during the first phase of processing, indicating that the responses in extrastriate visual areas during this phase are determined by the feedforward progression of activity initiated in V1. The first responses occurred during the second processing phase, in the ipsilesional high-level visual areas. The activity then spread forward toward higher-level areas and backward toward lower-level areas. However, in contrast to responses in the intact hemisphere, the back-propagated activity in the early visual cortex did not exhibit the classic retinotopic organization and did not have well-defined response peaks.

Introduction

A substantial portion of conscious vision is mediated by the geniculostriate visual pathway, which relays visual information from the retina to the primary visual cortex (V1) and then to the extrastriate cortices. The cortical processing in this pathway begins in V1 at about 40–50 ms post-stimulus onset and proceeds rapidly through low- and mid-level retinotopic extrastriate areas (V2–V5) (Grill-Spector and Malach, 2004; Lamme and Roelfsema, 2000; Poghosyan and Ioannides, 2007). Within the first 100 ms after stimulus exposure activity spreads beyond the retinotopic areas proceeding toward high-level, largely non-retinotopic visual areas (Ioannides and Poghosyan, 2012; Liu et al., 2009; Meeren et al., 2008; Okazaki et al., 2008). The second phase of activity through the same areas occurs in the next 100 ms interval (Ioannides and Poghosyan, 2012; Meeren et al., 2008; Sugase et al., 1999). Within each phase cortical processing begins in V1 and traverses the visual cortical hierarchy (Ioannides and Poghosyan, 2012).

Substantial visual processing is also mediated by the extra-geniculostriate pathways that bypass V1 and project directly to the extrastriate cortex. In fact, patients with cortical blindness following damage to V1 can retain some residual visual capability in the absence of awareness ("blindsight" phenomenon) (Poppel et al., 1973; Weiskrantz, 2009b; Weiskrantz et al., 1974). Hemianopic patient GY, who sustained selective early damage to his left V1 can effectively discriminate stimuli presented in his (right) blind hemifield (Cowey and Stoerig, 2004; de Gelder et al., 1999; Schurger et al., 2006; Tamietto et al., 2009, 2010; Weiskrantz et al., 1995; Zeki and Ffytche, 1998). Neuroimaging studies on patient GY have found that his intact right occipital lobe and the intact portions of his left (lesioned) occipital lobe show conventional retinotopic organization (Baseler et al., 1999). However, when stimuli are presented

Abbreviations: MFT, magnetic field tomography; RAC, regional activation curve; SP, signal power; UVM, upper vertical meridian; LVM, lower vertical meridian; LHM, left horizontal meridian; RHM, right horizontal meridian; UR, upper right; LR, lower right; UL, upper left; LL, lower left; MOG, middle occipital gyrus; STS, superior temporal sulcus; MTG, middle temporal gyrus.

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in the blind hemifield, activity is restricted to dorsal and/or ventral extrastriate areas and shows abnormal retinotopic organization (Barbur et al., 1993; Goebel et al., 2001; Sahraie et al., 1997; Tamietto et al., 2010; Zeki and Ffytche, 1998).

Notably, however, no study has identified the precise spatiotemporal sequence of visual cortical responses following presentation of stimulus in the cortically blind hemifield, or has directly contrasted these spatiotemporal profiles with those elicited by the same stimuli in the intact hemifield. Furthermore, it is not yet known when and where the first such cortical response appears, or how it spreads thereafter along the adjacent cortical areas, and what, if any, is the causal contribution of V1 to this activity.

In the present study we used magnetoencephalography (MEG) together with a distributed source model (Ioannides et al., 1990; Taylor et al., 1999) to estimate with millisecond time accuracy the spatiotemporal properties of neural activity elicited by checkerboard-pattern stimuli placed in different portions of the visual field. We first documented the key spatiotemporal features of visual stimulus processing in three normal subjects, substantially extending the analysis of data reported earlier (Poghosyan and Ioannides, 2007). We then described the neural processing in the intact and damaged hemisphere of GY in response to the same stimuli and in reference to that of the three control subjects.

Methods

Subjects

Patient GY

GY is a 56-year-old man with right hemianopia and "blindsight" following selective damage to his left V1 suffered at the age of 7, as the result of a traumatic brain injury. GY's visual system has been previously tested in behavioral and psychophysiological experiments, as well as with fMRI and diffusion-tensor imaging methods, see (Baseler et al., 1999; Goebel et al., 2001; Tamietto and de Gelder, 2010; Tamietto et al., 2010). The procedure used to map GY's visual field in the current study is described in Supplementary methods.

The MEG experiment with GY was conducted at the MEG unit of the ULB-Hôpital Erasme, Brussels. The resident ethical committee approved the study, which was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. GY gave informed consent to participate in the study.

Controls

Three healthy right-handed male subjects aged 26–28 years, participated in the MEG experiment. All had normal vision. For each subject, the experiment was repeated on three different days. All experiments with normal subjects were conducted at RIKEN Brain Science Institute in Wako-shi, Japan. RIKEN's ethics committee approved the study, and all the subjects gave informed consent. In an earlier publication (Poghosyan and Ioannides, 2007) we reported the analysis of the averaged data from a subset of the runs from this experiment with emphasis on the reproducibility of the results across different experimental days.

Stimuli and experimental design

Patient GY

GY was comfortably seated in a magnetically shielded room (MSR). The stimuli were delivered via a DLP projector (Model PT-D7700E, Panasonic, New Jersey, USA) located outside the MSR. Images were back-projected on a screen inside the MSR via an optical periscope.

Nine different locations of the visual field were stimulated, one at a time, using circular checkerboard patterns. The same parameters were used as for the control subjects for luminance and contrast levels (see Controls section), with slight modifications in size and locations made to ensure that the stimuli presented in the right visual hemifield fell entirely within the blind field of GY. Specifically, each stimulus had a radius of 4° and a check size of 1° (Fig. 1A). Normally the stimuli were presented centered on the visual vertical meridian (3.6° above and below the fixation), horizontal meridian (10° to the left and right of the fixation) and in the visual field quadrants 10° horizontally and 3.6° vertically off the visual meridians: on the upper vertical meridian (UVM), lower vertical meridian (LVM), left horizontal meridian (LHM) and right horizontal meridian (RHM), and in the upper right (UR), lower right (LR), upper left (UL) and lower left (LL) visual field quadrants. The central (near-foveal) stimulus was centered 1.5° to the left of the fixation in order to be entirely within the intact portion of the visual field. The stimulus in the UR quadrant was centered slightly closer (1°) to the horizontal meridian (at 2.6° above the meridian) than the homologous stimulus in the UL quadrant. In this work we focus on the

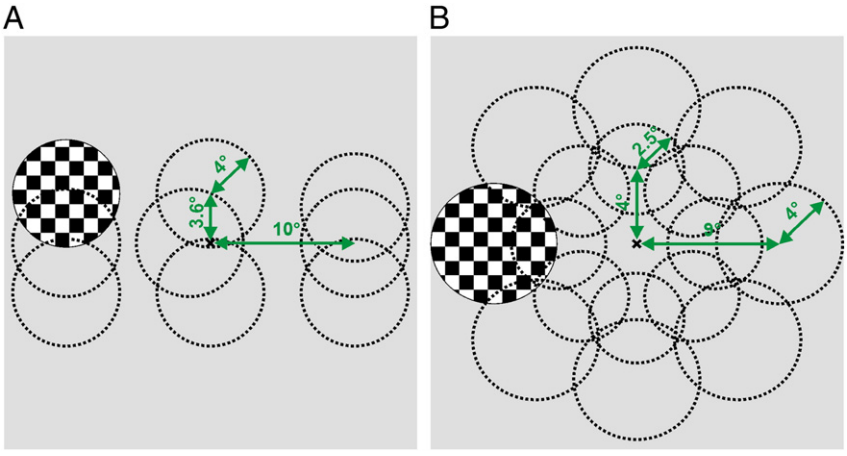

Fig. 1. Schematic image of stimuli. A. Stimuli used in the experiment with GY. Circular checkerboard patterns with radius of 4° were presented one at a time on the vertical and horizontal visual meridians, and in each quadrant of the visual field. Normally the stimuli were placed along the vertical lines passing through the central fixation (visual vertical meridian), and 10° to left and right of it; and along the horizontal lines passing through the central fixation (visual horizontal meridian), and 3.6° above and below it. The stimulus at the fixation (fovea) was centered 1.5° off the fixation into the left visual field so as to fall entirely in the intact portion of the visual field. The stimulus in the upper right quadrant was centered at 10° to the right of the fixation (as the normal stimuli) and at 2.6° above it. All stimuli had a check size of 1°. B. Stimuli used in the experiments with controls. Circular checkerboard patterns with radii of 2.5° and 4° were presented one at a time on the vertical and horizontal visual meridians, and in each quadrant of the visual field along its 45° diagonals in random order at 4° and 9° eccentricities, respectively. All stimuli had a check size of 1°.