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The evolution of a disparity decision in human visual cortex

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ABSTRACT

We used fMRI-informed EEG source-imaging in humans to characterize the dynamics of cortical responses during a disparity-discrimination task. After the onset of a disparity-defined target, decision-related activity was found within an extended cortical network that included several occipital regions of interest (ROIs): V4, V3A, hMT+ and the Lateral Occipital Complex (LOC). By using a response-locked analysis, we were able to determine the timing relationships in this network of ROIs relative to the subject's behavioral response. Choice-related activity appeared first in the V4 ROI almost 200 ms before the button press and then subsequently in the V3A ROI. Modeling of the responses in the V4 ROI suggests that this area provides an early contribution to disparity discrimination. Choice-related responses were also found after the button-press in ROIs V4, V3A, LOC and hMT+. Outside the visual cortex, choice-related activity was found in the frontal and temporal poles before the button-press. By combining the spatial resolution of fMRI-informed EEG source imaging with the ability to sort out neural activity occurring before, during and after the behavioral manifestation of the decision, our study is the first to assign distinct functional roles to the extra-striate ROIs involved in perceptual decisions based on disparity, the primary cue for depth.

Introduction

For primates, one of the main cues to depth perception is horizontal disparity, the difference between the retinal coordinates of a given feature. Over the last decades, the cortical mechanisms for disparity processing have been well investigated in macaque using single-cell recording (Cumming and DeAngelis, 2001; Hubel and Wiesel, 1970; Poggio and Poggio, 1984) and in human using fMRI (Backus et al., 2003; Durand et al., 2009; Neri et al., 2004). Disparity processing is important for perception and action (Melmoth and Grant, 2006), but the neural basis of its contribution to behavior is poorly understood. Electrophysiological studies, supported by microstimulation in the recorded areas, have demonstrated causal effects in both ventral and dorsal visual pathways in the decision process for various disparity tasks (DeAngelis et al., 1998; Shiozaki et al., 2012; Uka and DeAngelis, 2006). However, only a few areas have been explored, and none of the single-cell studies have recorded neural responses from multiple areas at the same time, making it difficult to characterize the entire cortical network involved in disparity-based decisions. With its high spatial resolution and large field of view, fMRI permits precise localization of the areas whose responses are related to disparity judgments (Chandrasekaran et al., 2007). However, the slow dynamics of the BOLD response does not allow precise characterization of the sequence of activity leading to the subject's response. Given its temporal resolution on the order of milliseconds, a technique like EEG may provide a better tool for deciphering the temporal characteristics of decision-making. EEG has been used to investigate perceptual judgments in various tasks (Philiastides and Sajda, 2006; VanRullen and Thorpe, 2001), including disparity tasks (Kasai and Morotomi, 2001). These studies have analyzed evoked responses at the scalp, which makes it challenging to determine the cortical areas involved in the decision.

In the current study, we used a high-density EEG imaging technique, which when coupled to fMRI-defined regions of interest (ROIs), allowed us to examine the dynamics of the responses directly at the cortical level (Cottereau et al., 2012a). The subjects performed a reaction-time disparity discrimination task. We were particularly interested in the decision-related activity within those ROIs whose disparity tuning properties we had previously characterized: V1, V4, V3A, Lateral Occipital Complex (LOC) and hMT+ (Cottereau et al., 2011, 2012b,c). Using a response-locked analysis (see also Ales et al., 2013), we were able to establish that among our five visual ROIs, the V4 ROI is the first to exhibit decision-related activity. We also found that all the extra-striate visual areas exhibit significant post-decision activity.

Materials and methods

Subjects

The 11 participants (6 males, 5 females, age range, 24–69 years) were volunteers, with normal stereopsis and normal or corrected-to-

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normal visual acuity. They were given instructions and detailed information about the experiments and provided written informed consent before participating in the study in accordance with Helsinki Declaration; the human subjects review committee of the Smith-Kettlewell Eye Research Institute approved the study.

Stimulus display

Stereoscopic stimuli were displayed using a system in which orthogonally polarized images from two matched Sony Trinitron monitors (Model 110GS), were combined via a beamsplitter and viewed through appropriately oriented polarized filters placed immediately in front of the eyes. Each eye could see the image from only one screen; the viewing distance was 80 cm. Each screen had a resolution of 1024 by 768 pixels and was refreshed at 85 Hz. The luminance of the background was 4.52 cd/m^2. The luminance of the dots was 85.88 cd/m^2.

Experimental protocol

The task consisted of a disparity discrimination judgment. The base stimulus (Fig. 1) was a 7.5-degree diameter central disk, surrounded by a large annulus (15 degree diameter); both were composed of dynamic random dots (90% contrast) that were refreshed every 47 ms (21.25 Hz). Each dot consisted of a square of 6.5 arcmin on a side. The dot density was 30 dots per square degree of visual angle. The central disk alternated at 1 Hz (square wave) disparity value was increased to between a fixed crossed disparity of 5 arcmin and the fixation plane (0 arcmin). Intermittently (30% of time), the disparity value was increased to $(5 + \delta d)$ arcmin ("Odd step"). The subjects were asked to detect these changes by pressing a button with their right index finger. The disparity value of the non-target stimuli was the same for each subject and was set to 5 arcmin. The size of the odd step δd was determined individually prior to the EEG session in order to obtain 80% correct discrimination of the incremental change in disparity ('Hits'). Subjects did not receive feedback regarding the correctness of their responses.

To facilitate fusion of the two monocular images, the stimuli also contained a pair of nonius lines (one in each eye) and a binocularly visible fixation point superimposed on the center of the disk-annulus (see Fig. 1). These nonius lines, combined with the fixation point and the large static annulus constituted a stable zero-disparity reference that permitted the subjects to maintain their fixation at the horopter during the disparity step of the disk. To assess the stability of fixation, we asked our subjects if they experienced misalignment of the nonius lines during the recordings. All of them reported that the lines remained aligned. Given that the sensitivity for nonius misalignment is typically below 2 arcmin (McKee and Levi, 1987), we conclude that eye position was not driven by the stimulus. Previous psychophysical measurements of fixation stability (Cottereau et al., 2011) confirmed that subjects can hold their fixation during the type of disparity modulations presented here. The recordings were performed in blocks of continuous trials that lasted 11 s (i.e. 11 trials per block). No odd steps were displayed during the first second. There was at least one non-target trial between two odd step trials. The inter-block interval was 1 s. For each subject, data collection was continued until the subject reached at least 300 Hits, which typically led to recording sessions of roughly 45 min.

EEG signal pre-processing

The electroencephalogram (EEG) data were collected with 128-sensor HydroCell Sensor Nets (Electrical Geodesics, Eugene OR) and were band-pass filtered from 0.3 to 50 Hz. EEG artifacts were eliminated off-line using standard procedure whose description can be found in Cottereau et al. (2012c). Before the source imaging procedure (see the fMRI-informed inverse modeling of the cortical currents section), data were segmented into one-second trials corresponding to one full cycle of the 1 Hz disparity display. At $t = 0$, the center disk is presented with either a crossed disparity of 5 or $(5 + \delta d)$ arcmin for 500 ms and then is returned to the fixation plane for another 500 ms. These one-second trials were baseline corrected by subtracting the average activity over the 100 ms directly preceding their beginning. Trials corresponding to the first second of the stimulus were discarded from the analysis, as they never contain the odd step. The remaining trials were then sorted into four distinct categories: 1) Hits (correct detection of a target), 2) Misses (missed target), 3) Correct Reject (correct detection of a non-target disparity) and 4) False alarms (detection of a non-target disparity). As we will see in the Results section, the number of false alarms was too small to permit a proper analysis. This category is therefore not discussed in this study. The Hit responses were also analyzed after temporal alignment to the button press. In this case, trials consisted in 1 s centered on the subject's response. Once again, these trials were baseline corrected by subtracting the average activity over the 100 ms directly preceding the stimulus onset (i.e. before alignment to reaction time). To eliminate the contribution due to the random dot refresh-rate ($f = 21.25$ Hz), all data were low-pass filtered at 20 Hz using a zero-phase filter. Because filtering can affect the estimation of onset latencies (VanRullen, 2011) the timing described in this study

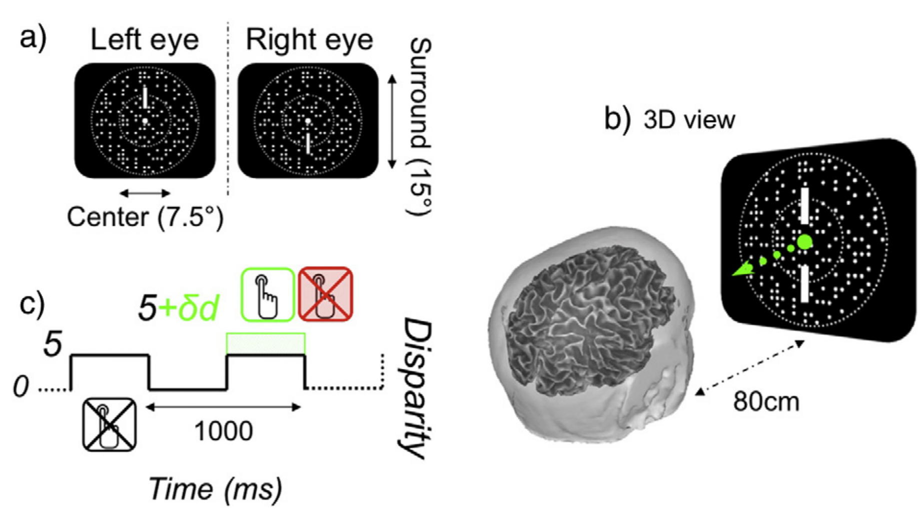

Fig. 1. Experimental protocol. a) Left and right monocular images used to define the center-surround display. Nonius lines are provided above (left eye) and below (right eye) the fixation point to facilitate fusion. The dots are refreshed at 21.25 Hz. b) 3D view of the stimulus. c) Temporal properties. The disk moves between 0 and 5 arcmin (crossed domain) at 1 Hz. 30% of the time, the disparity increment equals $(5 + \delta d)$ arcmin and the subject has to detect the event and press the button.