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Activity in high-level brain regions reflects visibility of low-level stimuli

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ABSTRACT

Stimulus visibility is associated with neural signals in multiple brain regions, ranging from visual cortex to prefrontal regions. Here we used functional magnetic resonance imaging (fMRI) to investigate to which extent the perceived visibility of a “low-level” grating stimulus is reflected in the brain activity in high-level brain regions. Oriented grating stimuli were presented under varying visibility conditions created by backward masking. Visibility was manipulated using four different stimulus onset asynchronies (SOAs), which created a continuum from invisible to highly visible target stimuli. Brain activity in early visual areas, high-level visual brain regions (fusiform gyrus), as well as parietal and prefrontal brain regions was significantly correlated with subjects' psychometric visibility functions. In addition, increased stimulus visibility was reflected in the functional coupling between low and high-level visual areas. Specifically, neuroimaging signals in the middle occipital gyrus were significantly more correlated with signals in the inferior temporal gyrus when subjects successfully perceived the target stimulus than when they did not. These results provide evidence that not only low-level visual but also high-level brain regions reflect visibility of low-level grating stimuli and that changes in functional connectivity reflect perceived stimulus visibility.

Introduction

Does activity in high-level brain regions reflect perceived visibility of a low-level visual stimulus? Here we investigated this question by modifying subjects' visibility of low-level target stimuli (here oriented Gabor gratings) using a visual masking procedure. It has been previously shown that changes in visibility are reflected in high-level brain regions using complex stimuli such as faces (Fahrenfort et al., 2012; Lumer et al., 1998), words (Dehaene et al., 2001), or complex shapes and objects (Grill-Spector et al., 2000; Haynes et al., 2005). Similarly, animal electrophysiology studies (Bridgeman, 1980, 1988; Kovacs et al., 1995; Lamme et al., 2002; Rolls et al., 1999) and recent human ERP and MEG studies (Dehaene et al., 2001; Del Cul et al., 2007; Fahrenfort et al., 2007; Melloni et al., 2007) suggested the involvement of high-level brain regions under visual masking conditions. However, the effect of perception of low-level stimuli on signals in high-level regions has been only rarely addressed (Tse et al., 2005). Hence, we investigated whether high-level brain regions reflect changes in subjects' perceived visibility using low-level grating stimuli and visual masking. In addition, we investigated functional coupling between different visual brain regions under different visibility conditions. This has been only rarely studied in the context of visual awareness and perceived visibility (Dehaene et al., 2001; Fahrenfort et al., 2012; Haynes et al., 2005; Imamoglu et al., 2012; Lumer and Rees, 1999).

We used backward visual masking by noise to study changes in subjects' perceived visibility and how these changes are reflected in neuroimaging brain signals. Visual masking is a widely used procedure to manipulate the perceived visibility of a stimulus (Breitmeyer and Ögmen, 2006; Bridgeman, 1980; Grill-Spector et al., 2000; Macknik and Livingstone, 1998; Rolls et al., 1999). Backward masking by noise is one visual masking type in which the visibility of one briefly presented target stimulus (here a left- or right-tilted grating, Fig. 1 and S1A) is followed by a temporally succeeding briefly presented mask stimulus (here a random noise mask, see also Fig. 1 and S1B). By varying the stimulus onset asynchronies (SOAs), i.e., the delay between the target stimulus and the mask stimulus onset, perception of the target stimulus can be impaired (Breitmeyer and Ögmen, 2006). The psychometric visibility function reflects each subject's visibility profile. In a typical backward masking experiment this is an ascending function with

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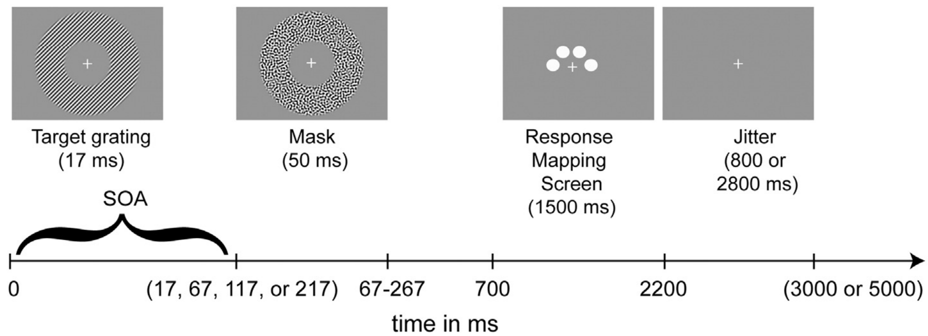

Fig. 1. Experimental design. A backward masking by noise experiment with four different visibility levels controlled by the four stimulus onset asynchronies (SOA; 17, 67, 117 or 217 ms) was used. The experiment started with the presentation of the target stimulus (right or left tilted grating) for 17 ms. A blank interval of 0, 50, 100 or 200 ms followed the target presentation that corresponded to the four SOAs respectively (17, 67, 117, or 217 ms). Subsequently, three consecutive different noise frames were presented for a total duration of 50 ms. A response mapping screen (duration 1500 ms) was presented 700 ms after the target onset. A subsequent jitter followed the response mapping screen, completing the total trial duration of 3000 ms or 5000 ms. Subjects' task was to indicate the orientation of the target grating by selecting the corresponding left or right tilted symbol during the response mapping screen using a left or right button press respectively.

increasing visibility levels (Type A masking function, (Kolers, 1962), see also Fig. 2). We used functional magnetic resonance imaging (fMRI) to search for activity in the human brain that followed the Type A psychometric visibility function. Furthermore, using a functional connectivity approach we examined whether the functional coupling in distant brain regions is correlated with changes in individual subject's perceived visibility profile. Our results suggest that not only early visual areas (V1–V4) but also high-level visual areas such as the fusiform gyrus and the superior occipital gyrus as well as a cluster including the superior parietal cortex and superior frontal gyrus are correlated with subjects' visibility profiles. Furthermore, increased stimulus visibility is reflected in increased functional coupling between the middle occipital gyrus and inferior temporal gyrus.

Materials and methods

Participants

Fourteen healthy subjects (six female, age range 21 to 36 years) participated in the experiment. All subjects had normal or corrected to normal vision and gave written informed consent to participate in the fMRI experiment. The experiment was approved by the Local Ethics Review Board of the Max Planck Institute for Human Cognitive and Brain Science (Leipzig) and conducted according to the Declaration of Helsinki. Three subjects were discarded from the analysis, one due to systematic motion during the experiment and two due to low performance in the behavioral task (Fig. S2).

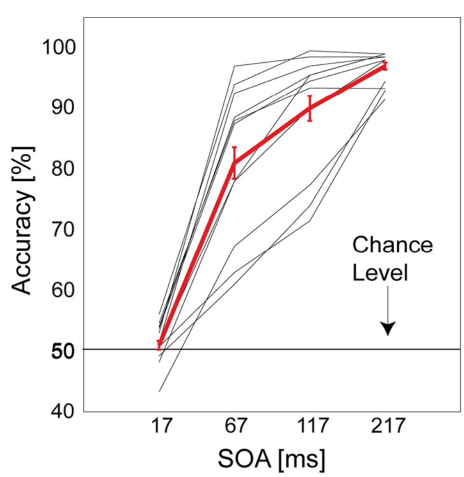

Fig. 2. Stimulus visibility. Subjects' psychometric visibility functions for 11 subjects that entered the fMRI analyses are shown. The x-axis represents the four visibility levels (SOA1 = 17 ms, SOA2 = 67 ms, SOA3 = 117 ms, SOA4 = 217 ms). The y-axis depicts the percent correct responses. The red bold line shows the mean curve with the error bars indicating standard error of the mean. A performance range from 50% correct answers (chance level) for the low-visibility condition (SOA1) to 100% correct answers for the high-visibility conditions (SOA4) indicates that the masking worked properly for all subjects.

Stimuli

The target stimuli were gratings of two orientations: right-tilted (45°) and left-tilted (135°). We used four different phase-shifts (0°, 90°, 180°, 270°) of these targets to minimize retinal adaptation (Fig. S1A). The spatial frequency of the gratings was 2 cpd (cycles per degree of visual angle). The contrast of the target stimuli was 0.3 (standard deviation of the pixelwise luminance divided by the mean luminance). The grating annulus covered the visual field from 4° to 9° eccentricity, sparing the fovea to enhance the stimulus masking effect. The noise mask (Fig. S1B) was created by bandpass filtered noise with the same peak spatial frequency as the spatial frequency of the oriented grating without any orientation preference. We employed a backward masking procedure where the mask was briefly flashed after the grating stimulus (for details on timing see below). The mask had a higher contrast (0.7) than the target stimulus. Three frames with different random versions of the mask were briefly flashed in succession after the grating stimulus for a powerful masking effect. All parameters of the visual stimuli were selected based on behavioral pre-tests.

Experimental procedure

We used backward pattern masking by noise, where visibility was manipulated by varying the stimulus onset asynchrony (SOA), which is defined as the time interval between the target and mask onsets. Four different SOAs were used to create a range from invisible to highly visible conditions.

Subjects were instructed to fixate on the white cross in the middle of the screen during the whole experiment (Fig. 1). At trial onset, a left- or right-tilted grating stimulus (target) was presented for 16.6 ms (corresponding to 1 frame at 60 Hz). After a short delay of 0, 50, 100 or 200 ms (corresponding to SOAs of 17, 67, 117 or 217 ms, i.e., 1, 4, 7 or 13 frames), a mask of three consecutive, different noise frames was flashed for a total duration of 50 ms. The four SOAs created four visibility conditions ranging from invisible (short SOA, 17 ms) to highly visible (long SOA, 217 ms). 700 ms after the trial onset a response mapping screen was presented for 1500 ms. This screen presented two symbols to the