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The levels of perceptual processing and the neural correlates of increasing subjective visibility

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ABSTRACT

According to the levels-of-processing hypothesis, transitions from unconscious to conscious perception may depend on stimulus processing level, with more gradual changes for low-level stimuli and more dichotomous changes for high-level stimuli. In an event-related fMRI study we explored this hypothesis using a visual backward masking procedure. Task requirements manipulated level of processing. Participants reported the magnitude of the target digit in the high-level task, its color in the low-level task, and rated subjective visibility of stimuli using the Perceptual Awareness Scale. Intermediate stimulus visibility was reported more frequently in the low-level task, confirming prior behavioral results. Visible targets recruited insulo-fronto-parietal regions in both tasks. Task effects were observed in visual areas, with higher activity in the low-level task across all visibility levels. Thus, the influence of level of processing on conscious perception may be mediated by attentional modulation of activity in regions representing features of consciously experienced stimuli.

1. Introduction

How do we become conscious of a brief visual stimulus? Is it the case that if one *sees* the stimulus, then one necessarily sees it in its entirety and all at once (Dehaene & Changeux, 2011), or is it the case that visual awareness affords degrees, so that one may have an imperfect (Overgaard, Rote, Mouridsen, & Ramsøy, 2006) or partial (Kouider, de Gardelle, Sackur, & Dupoux, 2010) impression of the stimulus? This question about the all-or-none vs. graded nature of visual experience also raises questions about the neural mechanisms that lead to conscious experience: Is there a "perceptual threshold" under which all stimuli remain unconscious, or is it the case that gradual changes in the neural activity in specific brain regions or networks lead to comparably gradual changes in visual experience?

Available empirical results appear to support both possibilities. In a series of studies, Overgaard and colleagues (Overgaard et al., 2006; Sandberg, Bibby, Timmermans, Cleeremans, & Overgaard, 2011; Sandberg, Timmermans, Overgaard, & Cleeremans, 2010) presented simple geometrical figures for different durations and asked participants to report their elementary features, such as color or shape. Subjective visibility was rated using the Perceptual Awareness Scale (PAS; Ramsøy & Overgaard, 2004), which involves four categories ranging from "no experience at all" to "clear experience", through two intermediate categories: "brief glimpse" and

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"almost clear experience". Based on the observed ratings, one can then build a psychometric function linking stimulus duration and subjective visibility. If visual awareness is all-or-none, one would expect this function to be almost like a step function, with a sharp transition between "no experience at all" and "clear experience" and few or no intermediate ratings. On the other hand, if visual awareness affords degrees, one would expect the slope of this function to be much shallower, as is the case for linear and logistic functions. It is the latter pattern that was generally observed in the aforementioned studies: relatively shallow psychometric functions, which support the idea that visual awareness is graded.

This account has been also supported by an fMRI study (Christensen, Ramsøy, Lund, Madsen, & Rowe, 2006), in which the same simple geometrical figures as in the aforementioned behavioral studies were used as stimuli and visibility was assessed with a three-point variant of the PAS scale ("no perceptual experience", "glimpse-like perceptual experience" and "clear perceptual experience"). Participants rated visibility of the stimulus on each trial. As in the behavioral studies, the distribution of subjective ratings supported a gradual account of changes in stimulus visibility as a function of duration. An increase of activity within the widespread network encompassing the precentral gyrus, intraparietal sulcus, basal ganglia and insula was observed, and followed gradual changes in visibility. Similar results were reported by Imamoglu, Heinzle, Imfeld, and Haynes (2014), who used backward masked low-level grating stimuli and found positive correlations between gradual changes in the psychometric visibility function and BOLD responses in low- and high-level visual areas, along with parietal and frontal cortices. For the aforementioned areas, the gradual changes in voxel activity were associated with gradual changes in participants' performance. However, due to the short interval between stimulus presentation and response, the design of this study makes it difficult to disentangle the strictly perceptual effects of stimulus visibility from the post-perceptual effects related to response generation (Aru, Bachmann, Singer, & Melloni, 2012). Further support for the gradual account comes from the electrophysiological studies of Sandberg and colleagues (Andersen, Pedersen, Sandberg, & Overgaard, 2016; Sandberg et al., 2013), demonstrating that N2-related components of the evoked-related potentials (or fields) can account for the observed gradual changes in visibility. Other neuroimaging studies using low-level stimuli indicate that the feedback activity in the early and the late visual areas is the possible process that underlies conscious visual perception (Fahrenfort, Scholte, & Lamme, 2007; Fahrenfort et al., 2012; Haynes, Driver, & Rees, 2005; Scholte, Jolij, Fahrenfort, & Lamme, 2008). These different observations all appear to lend support to the hypothesis that the mechanism of conscious visual perception involves recurrent processing in early and late visual areas (Lamme, 2010).

On the other hand, other studies typically using stimuli that require higher-level processing (e.g. semantic decoding) implied that conscious visual perception tends to be all-or-none. This is what was observed in a behavioral study using an attentional blink paradigm with number words as T2 targets embedded in a stream of four-consonant strings (Sergent & Dehaene, 2004). In order to assess visibility, the authors used the Sergent and Dehaene's Scale (SDS), consisting of 21 points, with end-points labeled "not seen" on the left and "maximum visibility" on the right side. Results showed that the frequency with which different points on the SDS scale had been used exhibited a bimodal distribution, with ratings having a tendency to cluster at the extreme points of this scale. The same method for assessing visibility was used by Del Cul and colleagues in a series of visual backward masking studies involving decisions about the magnitude of a masked digit (Del Cul, Baillet, & Dehaene, 2007; Del Cul, Dehaene, & Leboyer, 2006). In a forced-choice paradigm, participants were required to decide if the backward masked digit was larger or smaller than 5. Their results demonstrated that the nonlinear changes in the amplitude of the later positive ERP component, identified as P3, correlated with a steep increase in reported visibility as measured by the SDS scale. These results were interpreted in terms of recruitment of Global Neuronal Workspace (Dehaene & Changeux, 2011) – an extended network involving fronto-parietal regions assumed to be responsible for conscious processing (Dehaene, Charles, King, & Marti, 2014). Its nonlinear activation, metaphorically labeled "ignition", underlies abrupt changes in visibility evidenced in subjective reports in these studies (Dehaene et al., 2001).

In an attempt to reconcile these apparently contradictory findings, Windey and Cleeremans (2015), Windey, Gevers, and Cleeremans (2013), Windey, Vermeiren, Atas, and Cleeremans (2014) suggested that the level of processing required by the task can be a potentially important factor that influences the way in which we become conscious of visual stimuli. According to the Level-of-Processing hypothesis, the extent to which conscious perception is graded vs. all-or-none depends on the level of processing required by the task: experimental paradigms that require participants to make decisions about low-level features of the stimuli (e.g., color, shape) will yield gradual changes in subjective awareness as a function of stimulus quality (i.e., duration, contrast); whereas paradigms that require decisions about high-level, abstract features (i.e., magnitude, semantics) will afford stepwise changes in subjective awareness. In their studies, Windey, Gevers, and Cleeremans (2013), Windey, Vermeiren, Atas, and Cleeremans (2014) demonstrated that simply changing the experimental task from low-level (e.g. color discrimination) to high-level (e.g. number magnitude processing), while keeping the stimulus identical, can elicit noticeable differences in the behavioral markers of visibility, such as (1) the slope of psychometric function (Windey, Gevers, & Cleeremans, 2013), (2) the interaction between subjective visibility scale scores and behavioral performance (Windey, Vermeiren, Atas, & Cleeremans, 2014), or (3) the frequency of intermediate visibility ratings when using the PAS scale (Anzulewicz et al., 2015). Such differences, according to the authors, reflect distinct modes of transition from unconscious to conscious processing: more gradual for low-level stimuli and more dichotomous for high-level stimuli.

Here, in an attempt to test the Level-of-Processing hypothesis without relying exclusively on subjective reports and on behavior, we aimed at exploring the neural correlates of the differences between low-level and high-level processing in an fMRI study.

Documenting interactions between the changes in neural activity that accompany increasing visibility and the level of processing might be strong evidence in favor of the Level-of-Processing hypothesis. On the other hand, failure to detect such interactions would show that the observed behavioral differences might be caused by processes that are not directly associated with conscious perception (e.g. the influence of the level of processing on decisional processes, such as sampling of sensory evidence during response selection).

Therefore, we adapted the procedure from the study by Windey et al. (2013) for an event-related fMRI paradigm by controlling for the possible effects of the level of processing on the neural correlates of visual awareness at various stages of subjective visibility.