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# Functional hierarchies of nonconscious visual processing

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ABSTRACT

A number of psychophysical techniques can be used to eliminate the registration of stimuli in visual awareness and to study the dynamics of conscious and nonconscious information processing in the visual system. However, little is known about how these techniques relate to each other. We chose to compare binocular rivalry, induced by orthogonal gratings presented separately to the two eyes, and metacontrast suppression, produced when a target stimulus is followed by a spatially surrounding mask stimulus, to investigate relative levels and correlates of nonconscious processing. Combined with prior results, our findings indicate that binocular rivalry expresses its suppressive effects prior to the level at which the mechanism of metacontrast does. Implications for theories of masking and interpretations of the loss or perceptual effects when stimulus visibility is suppressed by different psychophysical methods are discussed.



## 1. Introduction

An increasing array of psychophysical techniques is available to psychologists and neuroscientists for rendering visual stimuli invisible (rev. Kim & Blake, 2005). These techniques are particularly useful in probing neural signatures of nonconscious as well as conscious visual processing (Dehaene et al., 2001; Dehaene, Sergent, & Changeux, 2003; Haynes, Driver, & Rees, 2005b; Koch, 2004; Kreiman, Fried, & Koch, 2005; Leopold, Murayama, & Logothetis, 2003; Wilke, Logothetis, & Leopold, 2003). However, very little is known about how these methods relate to each other and where, relative to each other, their suppressive effects occur during visual information processing. Here we begin exploration of such relations by examining the relative functional loci of the suppressive effects produced by two such methods, binocular rivalry and metacontrast.

Our rationale for pursuing this line of research is based on the following. Cortical nonconscious processing is a multi-level process that functionally precedes the level of processing correlated with conscious vision. Any of the above methods, by rendering stimuli inaccessible to conscious processing, exert their suppressive effects at stages of neural processing that functionally are at or lower than those stages correlated uniquely with conscious processing. Exerting their suppressive effects after the stage of conscious stimulus processing is a contradiction of terms since the activation of a functional level correlated with conscious processing will, by definition, imply conscious registration of the stimulus. Likewise, we argue that if one of the above methods, Method 1, renders a stimulus not only inaccessible to conscious report but also suppresses the mechanism by which another method, Method 2, renders a stimulus inaccessible to consciousness – in effect restoring the visibility of the suppressed stimulus – then the Method 1's suppressive mechanism exerts its effect prior to or, at the latest, at the level of Method 2's suppressive mechanism.

Like nonconscious processing, binocular rivalry is a complex multi-stage phenomenon (Blake & Logothetis, 2002). The use of a large variety of rivalry-inducing stimuli has revealed a hierarchy of cortical processes involved in binocular rivalry (Lee, Blake, & Heeger, 2007; Tong, Meng, & Blake, 2006). Although there are suggestions for a low-level interocular inhibitory component in binocular rivalry (Haynes, Deichmann, & Rees, 2005a; Lee & Blake, 2002; Tong et al., 2006; Wunderlich, Schneider, & Kastner, 2005; Wilson, 2003), there also is evidence that high-level processes such as attention, object-recognition and perceptual-grouping can, e.g., via feedback, modulate the expression of binocular rivalry (Blake & Logothetis, 2002; Kovács, Papathomas, Yang, & Fehér, 1996; Lee & Blake, 2004; Lee et al., 2007; Tong et al., 2006). Moreover, the depth of suppression increases as one proceeds along the cortical pathway (Nguyen, Freeman, & Alais, 2003; Scheinberg and Logothetis, 1997).

In the present experiments, binocular rivalry will be induced by dichoptic viewing of orthogonal gratings. Simultaneous presentations of, say, a vertical grating to the left-eye and a horizontal grating to the right eye (see Fig. 1) results in interocular competition

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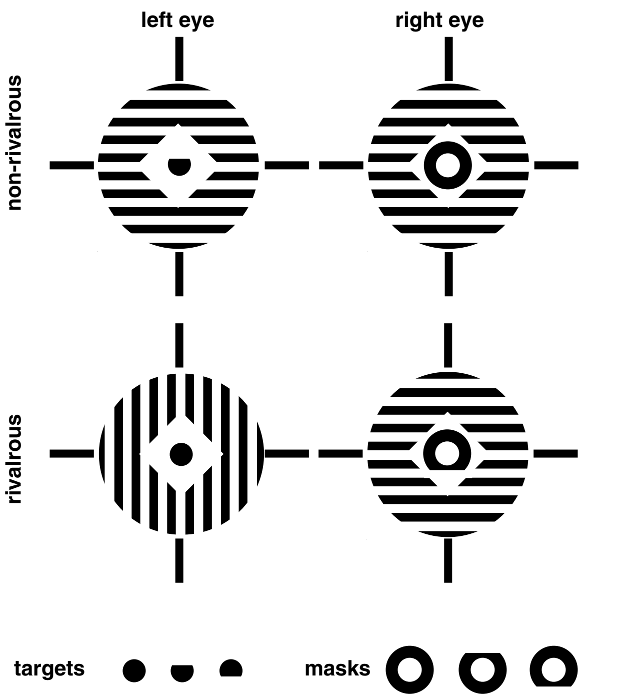


**Fig. 1.** Left-eye and right-eye stimulus displays. Upper panel: in the non-rivalrous dichoptic viewing condition, the same horizontal grating displays are presented to both eyes. Middle panel: in the rivalrous dichoptic viewing condition, a vertical and a horizontal grating display are presented to the left and right eye, respectively. Lower panel: on any trial, one of three target stimuli and one of three mask stimuli were presented to the left and right eye, respectively.

and rivalry for perceptual dominance. Observers report alternating periods during which the input to one eye is perceptually dominant while that of the other eye is suppressed (Alais & Blake, 2005). Stimuli such as these orthogonal gratings are believed to strongly activate low-level rivalry mechanisms, presumably located as early as V1 (Lee et al., 2007; Wilson, 2003). This is supported by findings that, compared to perceptual rivalries such as Necker-cube reversals, binocular rivalry induced with orthogonal gratings are largely stimulus driven and therefore relative immune to high-level modulation such as selective attention or voluntary control (Meng & Tong, 2004; van Ee, van Dam, & Brouwer, 2005). Henceforth we will refer to these as the low-level binocular rivalry (B-R) mechanisms. In metacontrast suppression, the visibility of a brief target, such as the disk-like stimuli shown in Fig. 1, is suppressed maximally when a brief surrounding mask ring follows the target by 40–60 ms (Breitmeyer & Öğmen, 2006). The resulting percept is of a mask without a target.

With either method one can investigate various types of neural processing that fail to register in phenomenal awareness. Like binocular rivalry, metacontrast suppression, one of several types of visual masking (Breitmeyer & Öğmen, 2006), involves cortical processes, since (a) it is obtained with dichoptic viewing, i.e., when the target is presented to one, and the mask to the other, eye (Kolers & Rosner, 1960; Schiller & Smith, 1968) and (b) neuro-imaging techniques have shown involvement of cortical sites (Haynes et al., 2005b). Important for the development of our argument is the additional fact that a metacontrast mask, M1, can suppress the target's visibility even when its own visibility in turn is suppressed by a second larger mask, M2, which surrounds and follows M1 at an optimal metacontrast delay (Breitmeyer, Rudd, & Dunn, 1981; Öğmen, Breitmeyer, Todd, & Mardon, 2006). When M1 is physically omitted and only the target and M2 are presented, the target is visible. This indicates that M2 on its own does not suppress the visibility of the target. Thus when M1 was present but its visibility was suppressed, it nonetheless generated neural activity that suppressed the target's visibility. This demonstrates that the neural process responsible for M1's masking effectiveness (a) acts at a nonconscious level of processing and (b) is dissociable from the neural processes underlying the conscious percept of M1. The question posed in the following experiment is: in the functional stream of visual processing, where relative to the nonconscious mechanism of metacontrast suppression does the mechanism of low-level B-R suppression reside?

## 2. Method

### 2.1. Participants

Four male volunteers ranging in age from 25 to 58 years participated as observers. Two of the observers were the authors BGB and AK; the other two observers were naïve, although practiced in making psychophysical judgments. All observers had normal binocular vision.

### 2.2. Stimuli and procedure

Visual stimuli were generated via the visual stimulus generator (VSG) card manufactured by Cambridge Systems (http://www.crsltd.com) and the stimuli were displayed on a 19″ high-resolution color monitor with a 100 Hz frame rate. The stimuli were displayed at a luminance of 0 cdm$^{-2}$ on a uniform, 25 cdm$^{-2}$ background. A head/chin rest was used to aid observer fixate at the center of the monitor. The distance between the monitor and the observer was set to 90 cm. Behavioral responses were recorded via a joystick connected to the computer, hosting the VSG card. Target and mask displays were presented on the left and right side of the monitor, respectively, and a stereoscopic mirror arrangement was used to present the target and mask stimuli separately (dichoptically) to the left and right eyes, respectively. The target and the mask were presented dichoptically in the center of white diamond fields surrounded by square-wave gratings as shown in Fig. 1. Both target and mask were presented for 20 ms. The onset asynchrony between the target and mask was set at 40 ms to provide maximal suppression of the target's visibility, as determined by a pilot experiment. In the non-rivalrous condition (Fig. 1, upper panel), both the left-eye target and the right-eye mask were presented in a central diamond-shaped region (25 cdm$^{-2}$) surrounded by horizontal gratings. In the rivalrous condition (Fig. 1, middle panel), the left-eye target and the right-eye mask were presented in a same central diamond-shaped region surrounded by a vertical and horizontal gratings, respectively. Gratings subtended a circular area having a diameter of 1.5° and the spatial frequency of the grating was six cycles per degree. White and black bars of the grating were 50 cdm$^{-2}$ and 0 cdm$^{-2}$, respectively, to yield the same space-averaged luminance of 25 cdm$^{-2}$ as the uniform background.

Vertical and horizontal fixation bars, comprising a notional fixation cross, were located adjacent to the grating areas to facilitate binocular fixation. Observers were instructed to fixate the center of the diamond-shaped field. In the rivalrous viewing condition, the observer pressed the left button of the joystick whenever the left-eye vertical grating dominated perception. Two hundred milliseconds later the target-mask sequence was presented. Since perceptual dominance of an eye's input is maintained for several seconds as shown in previous studies as well as in our pilot experiments, the visibility of the mask in the right eye was effectively suppressed.

On any trial, the target stimulus could be a whole disk or one with a lower or upper truncation (Fig. 1, lower left panel). Similarly, the mask stimulus could be a whole annulus or one with a lower or upper truncation (Fig. 1, lower right panel). The inner and outer diameters of the mask were 0.25° and 0.35°, respectively. The target had a diameter of 0.25°. Each observer was run in 16 blocks. In each block of 18 trials, two trials were devoted to each of the nine possible target-mask combinations. Eight blocks were devoted to the non-rivalrous control condition and eight blocks to the rivalrous condition. In each condition four blocks were devoted to identification of the target and four blocks to identification of the mask. Thus a total of 72 trials were used for each combination of viewing condition and stimulus-identification task. Order of identification tasks (target or mask) and viewing conditions (rivalrous or non-rivalrous) was counterbalanced across the four observers. The observer pressed one of the three buttons of the joystick indicating the shape of the target or the mask. Accuracy of the observers was recorded to determine the visibility function. In case of total invisibility of either the target or the mask, one would expect an observer to be correct by chance on 24 of the 72 trials.

## 3. Results

We hypothesized that the relationship between B-R and metacontrast suppression can take two forms. According to Hypothesis