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On the functional order of binocular rivalry and blind spot filling-in

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ABSTRACT

Binocular rivalry is an important phenomenon for understanding the mechanisms of visual awareness. Here we assessed the functional locus of binocular rivalry relative to blind spot filling-in, which is thought to transpire in V1, thus providing a reference point for assessing the locus of rivalry. We conducted two experiments to explore the functional order of binocular rivalry and blind spot filling-in. Experiment 1 examined if the information filled-in at the blind spot can engage in rivalry with a physical stimulus at the corresponding location in the fellow eye. Participants' perceptual reports showed no difference between this condition and a condition where filling-in was precluded by presenting the same stimuli away from the blind spot, suggesting that the rivalry process is not influenced by any filling-in that might occur. In Experiment 2, we presented the fellow eye's stimulus directly in rivalry with the 'inducer' stimulus that surrounds the blind spot, and compared it with two control conditions away from the blind spot: one involving a ring physically identical to the inducer, and one involving a disc that resembled the filled-in percept. Perceptual reports in the blind spot condition resembled those in the 'ring' condition, more than those in the latter, 'disc' condition, indicating that a perceptually suppressed inducer does not engender filling-in. Thus, our behavioral data suggest binocular rivalry functionally precedes blind spot filling-in. We conjecture that the neural substrate of binocular rivalry suppression includes processing stages at or before V1.

Binocular rivalry occurs when two eyes receive conflicting information that cannot be integrated into one single, coherent percept, and it refers to the alternations in perception between the two monocular inputs that ensue in this situation. Rivalry thus allows researchers to alter subjective awareness without altering the physical stimuli, because a physically present stimulus can become subjectively invisible when it is suppressed by its rivaling counterpart. As a consequence, binocular rivalry has become a popular tool to investigate visual awareness and consciousness (Crick & Koch, 1998).

Specifically, the neural basis of binocular rivalry is viewed as pertinent to identifying neural correlates of conscious awareness (Blake, Brascamp, & Heeger, 2014) and has been vigorously debated (Blake & Logothetis, 2002; Tong, Meng, & Blake, 2006; Wilson, 2003). Traditionally, one view, which may be called the low-level interocular competition view, supposes a central role for competition between the eyes, specifically between the monocular neurons in the primary visual cortex (V1; Blake, 1989; Tong, 2001; Tong & Engel, 2001; Tong et al., 2006) or lateral geniculate nucleus (LGN; Haynes, Deichmann, & Rees, 2005; Lehky, 1988; Wunderlich, Schneider, & Kastner, 2005). An alternative view holds that binocular rivalry is a phenomenon reflecting the competition between incompatible patterns beyond monocular levels of representation (Leopold & Logothetis, 1996; Logothetis, Leopold, & Sheinberg, 1996). Given the evidence in favor of each of these views, a consensus has emerged that binocular rivalry draws on several processing levels, and that its neural substrate might be influenced by the type of stimulus used (Tong et al., 2006; Wilson, 2003). Nevertheless, several recent results appear consistent with the idea that low-level mechanisms might be sufficient for the occurrence of binocular rivalry, as they suggest that binocular rivalry can occur without conscious awareness (Zou, He, & Zhang, 2016) and with negligible involvement of higher-level brain areas (Brascamp, Blake, & Knapen, 2015)[1].

Here we further explored the neural locus of binocular rivalry by assessing the functional stage of binocular rivalry in relation

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[1] We note, however, the outcome of binocular rivalry resolution might still require further processing before impacting subjective awareness, likely in cortical visual areas beyond V1 (e.g., Lee, Blake, & Heeger, 2007).

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to that of perceptual filling-in in the blind spot. Typically, during such filling-in, a stimulus that surrounds the location of the retinal blind spot gets perceptually filled in, so that the observer perceives the stimulus as continuous. In a certain sense, then, filling-in phenomena, which involve subjective awareness of a stimulus that is physically absent, are the converse of phenomena like binocular rivalry. Given that perceptual filling-in involves an internally generated representation in the absence of the physical stimulus (Komatsu, 2006), one of our questions was whether this internally generated representation could engage in rivalry competition. Similarly, we were interested in whether a perceptually suppressed stimulus could still lead to blind spot filling-in. These questions can inform us about the functional order of filling-in and binocular rivalry. Given that blind spot filling-in starts as early as V1 (Awater, Kerlin, Evans, & Tong, 2005; Júnior, Rosa, Gattass, & Rocha-Miranda, 1992; Komatsu, 2006; Matsumoto & Komatsu, 2005), filled-in information might be able to engender binocular rivalry, if rivalry occurs at or after filling-in is completed (e.g., V1). Based on our experiments, we can then draw tentative inferences regarding the neural site of rivalry by leveraging existing knowledge of the neural locus of filling-in (see below).

We conducted two experiments to explore the relationship between binocular rivalry and blind spot filling-in. Experiment 1 was intended to examine if the filled information (if any) at the blind spot can lead to rivalry with a physical stimulus at the corresponding area of the fellow eye (non-blind spot eye). To address this question, we compared the perceptual experiences that resulted during binocular rivalry in two conditions that either allowed for the possibility of blind-spot filling in, or that did not because the stimulus was displaced away from the blind spot. We reasoned that, if a filled-in blind-spot representation can engage in rivalry with the fellow eye, this would result in specific differences between the perceptual cycles experienced in these two situations. Otherwise, no difference between the two conditions was expected. Experiment 2 set the stimulus that surrounds the blind spot (the inducer) to be in rivalry with the fellow eye stimulus, therefore testing whether blind spot filling-in can occur, even while the observer is unaware of the inducer due to rivalry suppression.

1. Experiment 1

Here we examined whether putative filled-in information at the blind spot can rival with a physical stimulus by presenting a red inducer in one eye, termed the blind spot eye, and a green disc in the fellow eye (see Fig. 1a&b). The inducer was presented either at the blind spot location so that it could in principle give rise to a filled-in percept (called ON condition in Fig. 1a), or at an off blind spot control location (OFF condition in Fig. 1b). If a filled-in representation can engage in binocular rivalry, the ON condition would involve a filled-in red disc in rivalry with the green disc. The OFF condition, in contrast, involves an arrangement of a non-overlapping ring and disc. Our main measure of interest was the occurrence of what we call a 'hybrid percept' (Fig. 1d), i.e., the percept where a green disc (originating from the fellow eye) is seen surrounded by a red ring (originating from the blind spot eye). If the filled-in representation (if any) played a role in the ON condition, we expected to observe this percept less often in the ON than the OFF condition, because the filled-in disc would sometimes suppress the fellow eye's green disc in the ON condition, whereas in the OFF condition, the fellow eye's green disc would be paired with an empty gray area.

1.1. Methods

1.1.1. Participants

Fifteen participants were included in data analysis (10 females and 5 males; age: $M = 22.60$, $SD = 3.20$). One participant was the author (C.Q.), while the remaining were undergraduate and graduate students from Michigan State University who were naïve regarding the purpose of the experiment. All naïve participants signed a consent form and were compensated at a rate of $10/hour. All experimental protocols were approved by the Institutional Review Board at Michigan State University.

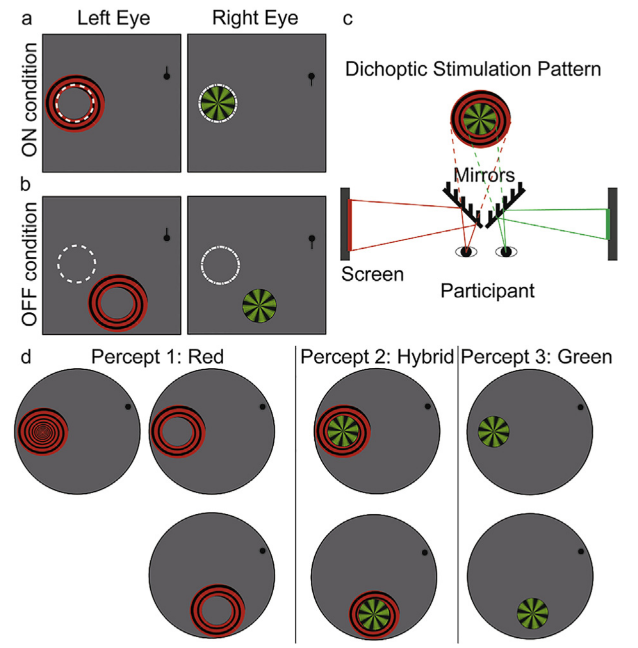

Fig. 1. (a&b) The physical stimuli, (c) experimental setup, and (d) percept categories of Experiment 1. (a) The ON condition: the inner edge of the ring was inside the blind spot (white dashed line). (b) The OFF condition: stimuli were presented away from the blind spot. Note the white dashed lines are for illustration purpose only; they were not presented during the experiment. (c) Experimental setup. (d) Possible percepts for Experiment 1. Participants reported percepts of red stimuli, hybrid stimuli, or green stimuli by holding one of three keys. The top row of this panel corresponds to the ON condition; the bottom row to the OFF condition. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

We excluded three participants in total. One participant was excluded for being unable to distinguish the color of the peripheral stimuli. Another showed unstable fixation indicated by the results of Experiment 2 (see below), and a third participant was excluded for reporting experiencing filling-in at the off blind spot location.

1.1.2. Materials

The experimental setup is a variant of the classical mirror stereoscope (Brascamp & Naber, 2016; Wheatstone, 1838), consisting of two mirrors (45° angle relative to participants' midline) reflecting stimuli from two screens facing each other (62 cm away from the midline of the participant). A head rest stabilized the alignment of participants to view the reflection of one mirror from each eye (see Fig. 1c for schematic illustration).

Visual stimuli were generated with PsychToolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). The fixation mark was composed of a black dot (0.36°) on both screens, one black line segment (0.12° in width and 1.20° in length) above the fixation dot presented to the left eye, and another line segment below the dot presented to the right eye. These separate segments above and below fixation and a binocularly presented square black frame (26.60° in size and 0.12° in width) guided the alignment of stimuli from the two screens. For the main experiment (see Fig. 1a–c), the left eye stimulus was a red annulus, whose inner edge fell inside the blind spot and whose outer edge fell outside the blind spot, which was localized before the main experiment (see below for procedure).