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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.

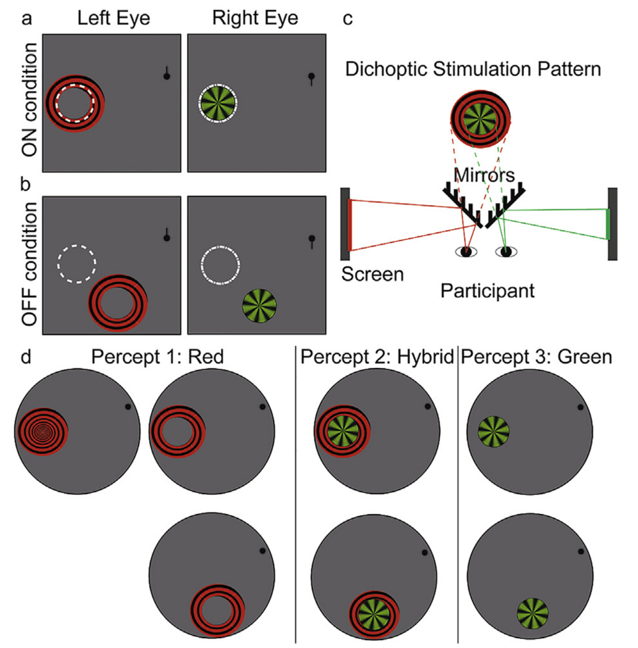

Fig. 1. (a&b) The physical stimuli, (c) experimental setup, and (d) percept categories of Experiment 1. (a) The ON condition: the inner edge of the ring was inside the blind spot (white dashed line). (b) The OFF condition: stimuli were presented away from the blind spot. Note the white dashed lines are 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).

The width of the annulus was equal to the radius of blind spot. The annulus contained a black-red spiral with two cycles in the polar dimension and four cycles in the radial dimension. The spiral stimulus rotated in the clockwise direction at a speed of 565° per second. The right eye stimulus was a green disc of the size of blind spot, positioned at the location corresponding to the center of the red annulus. The disc had a radial pattern of black-green wedges with four cycles in the polar dimension, rotating in the counterclockwise direction at a speed of 226° per second.

There were two conditions in this experiment. For the ON condition, the annulus was presented at the blind spot location of the left eye and the disc was presented at the corresponding (non-blind spot) location of the right eye. For the OFF condition, both stimuli were presented in a lower left location with the same eccentricity as the stimuli in the ON condition, but with their position rotated 60° counterclockwise around fixation.

1.1.3. Procedures

Participants stabilized their head on the chin rest, fixated on the fixation dot, adjusted the location of the fixation on one of the computer screens to align fixations from two screens (Carmel, Arcaro, Kastner, & Hasson, 2010), and ensured the alignment of the square black frames. Participants then moved, and adjusted the size of, a red disc presented only to their left eye to localize their blind spot. They first moved the red disc until it became invisible, then pressed keys to enlarge the disc until it became partially visible, and moved the disc again. Through several iterations of this process, they adjusted the disc until any increase in its size would render it visible. At this point, we identified the largest invisible disc as fully contained within participants' blind spot. Using this protocol, we found that participants' blind spot (in the left eye) was located in a lower left location relative to the fixation and was about six degrees wide (azimuth: $M = -11.77°$, $SD = 0.63$; elevation: $M = -1.63°$, $SD = 0.80$; radius: $M = 2.91°$, $SD = 0.31$), which was consistent with well-established measurements of the blind spot (Baek, Cha, & Chong, 2012; Maus & Whitney, 2016; Wandell, 1995).

There were two conditions in the main experiment: the red annulus and green disc were presented to two eyes dichoptically, either on the blind spot (ON) or off the blind spot (OFF). Each trial lasted for 65 s during which participants held down one of three keys to indicate their percept at any given moment: an entirely red stimulus, a green disc in the middle of a red annulus (the hybrid percept), or an entirely green stimulus (see Fig. 1d; note that the report method did not distinguish between an entirely red disc and an entirely red annulus). Before the main experiment, each participant performed one or two practice trial(s) to familiarize themselves with the task. Also before the experiment, the experimenter confirmed that participants saw a red disc when viewing the ON condition's left eye stimulus while their right eye stimulus was blocked, i.e., that normal blind-spot filling-in occurred on our setup. Participants completed four trials for each condition in a single experimental session that lasted 20 min.

1.2. Results and discussions

For every participant, the durations of individual key-holding epochs were summed for each of the three possible percepts (see Fig. 1d). Paired-sample t-tests were then conducted to compare the proportions of perceptual dominance for the three percepts.

By way of preliminary analysis we established that the proportion of time reporting the red stimulus was higher in the OFF condition than in the ON condition (ON: $M = 0.08$, $SD = 0.12$; OFF: $M = 0.31$, $SD = 0.17$; $t(14) = 4.29$, $p < 0.001$; see Fig. 2a), while the proportion of reporting the green stimulus is lower (ON: $M = 0.42$, $SD = 0.17$; OFF: $M = 0.28$, $SD = 0.20$; $t(14) = 2.30$, $p < 0.05$; see Fig. 2c). This is consistent with a previous study that also found lower rivalry strength for a stimulus that surrounds the blind spot (He & Davis, 2001), thus providing a further sanity check that we had localized the blind spot accurately.

As pointed out above, our critical dependent measure is the duration of the hybrid percept. The hybrid percept consists of the red ring stimulus from the left, blind spot, eye and the green disc stimulus from the right, fellow, eye. If the green disc in the ON condition experienced competition from a filled-in surface in the blind spot eye, then less occurrence of this hybrid percept would be expected for the ON condition than in the OFF condition, in which the non-overlapping ring and disc would not directly rival each other. Contrary to our expectation, the proportion of dominance of the hybrid percept did not show any reliable difference between the two conditions (ON: $M = 0.42$, $SD = 0.20$; OFF: $M = 0.34$, $SD = 0.14$; $t(14) = 1.54$, $p = 0.15$; see Fig. 2b). This lack of difference thus provided no evidence that the green disc in the ON condition experiences any competition from a filled-in surface. To assess the strength of evidence for the null hypothesis, we also conducted a Bayesian test (this analysis was conducted using JASP). The prior was set to be Gaussian distribution with no difference between ON and OFF conditions. The level of evidence for accepting the null hypothesis was considered "weak" (Bayes Factor = 1.44). Finally, we should note that the non-significant numeric difference was opposite to our expectation such that the ON condition showed a higher proportion of hybrid percept than the OFF condition.

To summarize Experiment 1, the relative proportions of perceiving the green and red stimuli were consistent with previous findings that a stimulus surrounding the blind spot acts as a weaker stimulus in binocular rivalry than the same stimulus away from the blind spot (He & Davis, 2001). Consistent with this idea, when we informally asked participants about their filled-in percept on the blind spot, they reported that the motion and texture in the blind spot was not as vivid as seeing a full disc in the OFF condition, which could account for an overall weaker dominance of the red percept compared to the green percept in the ON condition. Furthermore and critically, the predominance of the hybrid percept did not differ significantly between the ON and OFF conditions, providing no evidence that any filled-in information in the ON condition would compete in rivalry to a greater extent than the gray center in the OFF condition does. These results thus offer no support for the idea that any filled-in representation is present at a processing stage where binocular rivalry is resolved.

In evaluating the results of this first experiment, one possibility we considered is that a filled-in representation, even if it is present, might simply be too weak to provide much competition in rivalry with the physical stimulus from the fellow eye, preventing us from detecting any difference between the ON and OFF conditions in Experiment 1. In the second experiment, we therefore moved our focus away from rivalry involving a filled-in surface, to rivalry involving the inducer that may cause a filled-in surface. Of relevance to our overall question on the functional order of binocular rivalry and filling in, the main objective of this second experiment was to test whether the inducer can still engender filling in during periods when it is perceptually suppressed in rivalry.

2. Experiment 2

The stimuli of this experiment are illustrated in Fig. 3. A main change relative to Experiment 1 was that the fellow eye stimulus changed from a disc to a ring with the same dimensions as the inducer that was shown to the blind spot eye, in line with our new objective of studying perception while the inducer is engaged in rivalry. Moreover, we added a second ON condition where the inducing ring was physically filled in to form a disc (Fig. 3a, right).

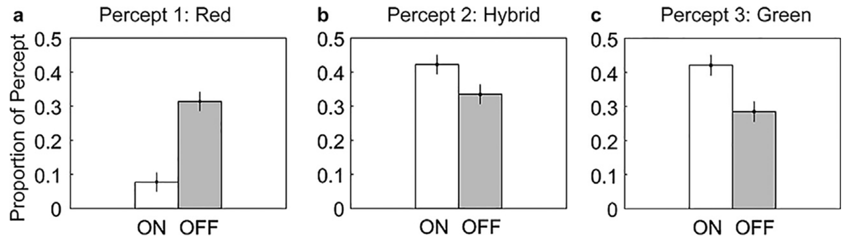

Fig. 2. Results for Experiment 1: proportions of reporting three percepts. Error bars are the estimated within-subject standard error following the method of Loftus and Masson (1994).

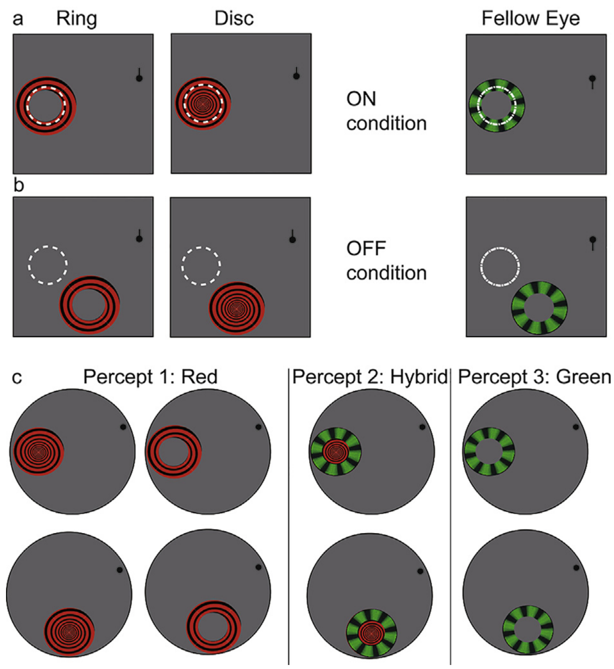

Fig. 3. The (a&b) physical stimuli and (c) possible percepts of Experiment 2. Participants reported percepts of red stimuli, hybrid stimuli, or green stimuli by holding one of three keys. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Because the absence of photoreceptors in the blind spot renders the sensory input in both these ON conditions identical, this second condition provided an internal control that we correctly localized the blind spot and that participants fixated steadily. If those two requirements were not met, then input differences between the two ON conditions could lead to differences in perceptual reports. Finally, we now included two OFF conditions instead of one: again, one involving a red ring of the same dimensions as the inducer (Fig. 3b, left), and one involving a physically filled-in red disc (Fig. 3b, right). As will be detailed below, these two OFF conditions provide two reference points for comparing the ON condition data; one corresponding to the hypothesis that there is no filling in while the inducer is suppressed, and one corresponding to the hypothesis that there is.

2.1. Method

2.1.1. Participants

The same participants from Experiment 1 participated in Experiment 2. We conducted independent sample *t*-test to compare the proportion of the hybrid percept in two ON conditions of each individual participant, one of whom exhibited a significant difference, indicating improper fixation or inaccurate blind spot localization and was excluded for further analysis.

2.1.2. Materials

The red disc had the same properties as the red ring in Experiment 1 except that the spiral motion spread throughout the whole circular area (eight cycles in the radial dimension). The green radial stimulus had the same radial spatial frequency and contrast as the green disc in Experiment 1, but the overall shape was that of a ring with the same spatial layout with the red ring (see Fig. 3a&b).

As in Experiment 1, the exact locations of physical stimuli were determined by the participants' blind spot localization procedure. The participants' blind spots fell to the lower left of fixation (azimuth: $M = -11.91°$, $SD = 0.90$; elevation: $M = -1.81°$, $SD = 0.79$; radius: $M = 2.87°$, $SD = 0.47$), consistent with well-established measurements about the blind spot.

2.1.3. Procedures

The experiment used a 2×2 design with Stimulus (Ring vs. Disc) and Location (ON vs. OFF blind spot) as factors. Participants pressed three keys to indicate their percept as they did in Experiment 1, as illustrated in Fig. 3c. The key difference is that the hybrid percept now consisted of red spiral motion in the center, surrounded by a green radial grating (see Fig. 3c, Percept 2). Practice was conducted to confirm participants' understanding of the task and blind spot localization (see Procedures for Experiment 1). Participants completed 4 trials (65 s per trial) for each condition in an interleaved fashion in a single session that lasted 40 min including rests.

2.2. Results and discussions

As was the case for Experiment 1, the critical dependent measure was the hybrid percept. The hybrid percept in this case involved the center of the red spiral appearing inside the green annulus. In the ON conditions, this percept would consist of a perceptually filled-in center combined with a surround that originates from the fellow eye. The hybrid percept should therefore take up an appreciable portion of time in the ON conditions, only if blind spot filling-in occurred while the inducer was suppressed in rivalry. The two OFF conditions provide indications of what 'appreciable' would mean here. Specifically, perception in the ON conditions should resemble that in the OFF ring condition if no such filling-in occurred, but it might match that in the OFF disc condition if filling-in did occur. We conducted an analysis based on two different measures of the hybrid percept's predominance: one is the absolute proportion of reporting the hybrid percept over the whole duration of the trial; the other one is a relative measure, namely the proportion of reporting the hybrid over the proportion of reporting either the hybrid percept or the green percept. The latter, relative measure is basically the proportion of seeing the red disc at the center, given that the green ring is visible. This measure

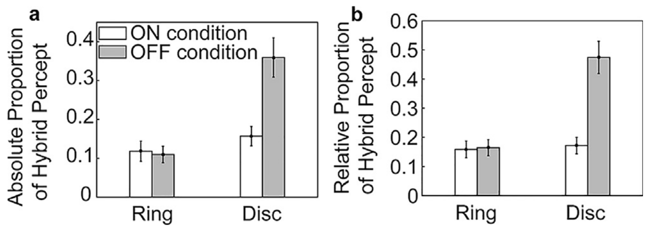

Fig. 4. Results of Experiment 2: (a) absolute measure and (b) relative measure of the proportion of the hybrid percept. Error bars are the estimated within-subject standard error following the method of Loftus and Masson (1994).

could control for possible differences in the predominance of the red stimulus between conditions.

We first verified that the two ON conditions produced indistinguishable perceptual sequences, as should be the case of observers kept steady fixation and thereby kept the ON-condition stimulus on the blind spot. This was, indeed, the case, at the group level ($t(14) = 0.89$, $p = 1.00$). At the individual observer level it was also true, except for one participant whose data was then discarded (see Methods). We then conducted a two-way repeated-measures ANOVA to assess the effect of stimulus (ring vs. disc) and location (on vs. off blind spot). The absolute proportion of seeing the hybrid (see Fig. 4a) was higher in the disc conditions than in the ring conditions ($F(1,14) = 13.23$, $MSE = 0.31$, $p < 0.01$) and higher in the OFF conditions than in the ON conditions ($F(1,14) = 6.25$, $MSE = 0.14$, $p < 0.05$) with a significant interaction ($F(1,14) = 9.05$, $MSE = 0.17$, $p < 0.01$). Post hoc comparisons based on Bonferroni correction showed that the OFF disc condition induced the highest proportion of seeing the hybrid percept, which drove both main effects and the interaction (OFF disc vs. OFF ring: $t(14) = 4.66$, $p < 0.001$; OFF disc vs. ON disc: $t(14) = 3.78$, $p < 0.01$; OFF disc vs. ON ring: $t(14) = 4.50$, $p < 0.001$; ON disc vs. ON ring: $t(14) = 0.89$, $p = 1.00$; OFF ring vs. ON disc: $t(14) = 0.88$, $p = 1.00$; OFF ring vs. ON ring: $t(14) = 0.16$, $p = 1.00$). The relative measure showed a similar pattern (see Fig. 4b) as the absolute measure, with a higher proportion in the OFF conditions than in the ON conditions ($F(1,14) = 9.07$, $MSE = 0.39$, $p < 0.01$), a higher proportion in the disc conditions than in the ring conditions ($F(1,14) = 17.24$, $MSE = 0.36$, $p < 0.001$), and a significant interaction ($F(1,14) = 18.43$, $MSE = 0.33$, $p < 0.001$). The post hoc comparisons also revealed that of all pair-wise comparisons, the only significant ones involve the OFF disc condition (OFF disc vs. OFF ring: $t(14) = 5.14$, $p < 0.001$; OFF disc vs. ON disc: $t(14) = 5.03$, $p < 0.001$; OFF disc vs. ON ring: $t(14) = 5.24$, $p < 0.001$; ON disc and ON ring: $t(14) = 0.22$, $p = 1.00$; OFF ring vs. ON disc: $t(14) = 0.12$, $p = 1.00$; OFF ring vs. ON ring: $t(14) = 0.10$, $p = 1.00$).

As pointed out above, the two OFF conditions established anchor points for interpreting results from the ON conditions: the disc condition constituted a situation where there was a physical surface in the center of the stimulus, while the ring condition constituted a situation where there was not. We found that the predominance of the hybrid percept was similar in the ON conditions and the OFF ring condition, while its proportion was higher in the OFF disc condition than all the other conditions. Thus, perception in the two ON conditions was similar to that in the OFF ring condition but different from that in the ON ring condition, suggesting that there was no blind spot filling-in during perceptual suppression of the inducer.

3. General Discussion

We conducted two experiments to examine the functional order of blind spot filling-in and binocular rivalry. In Experiment 1, the to-be-filled surface on the blind spot was not distinguishable, in terms of rivalry strength, from the gray center of the ring in the off blind spot control condition, which did not provide evidence that a filled in surface could engage in rivalry competition. In Experiment 2, we presented the filling-in inducer in direct rivalry with the fellow eye stimulus to examine if filled-in information could emerge when the inducer was perceptually suppressed. The results showed no such filling-in. These two experiments thus provide converging evidence for the conclusion that binocular rivalry suppression functionally precedes blind spot filling-in.

Previous studies have characterized the functional order of different visual suppression mechanisms by combining different suppression paradigms and measuring the perceptual outcomes (e.g., binocular rivalry and metacontrast masking; Breitmeyer, Koç, Öğmen, & Ziegler, 2008). Here, we used a similar logic to investigate the functional order of binocular rivalry, a suppression mechanism, and blind spot filling-in, which is a generating mechanism, as perceptual information is internally generated to compensate for the lack of sensory input. This allows us to leverage our understanding of the neural mechanism for filling-in to infer the locus of binocular rivalry, using the same type of reasoning others have used when combining different suppression mechanisms within the same paradigm. Although the specific pairing of binocular rivalry and blind spot filling-in is not common in existing work, one previous study did investigate this combination by positioning rivalry stimuli near the blind spot (He & Davis, 2001). Those authors used arrangements similar to ours but with the important difference that the inner edge of their ring inducer was outside the blind spot. As a consequence, their ON blind spot ring stimulus provided physically different input than their ON blind spot disc stimulus (i.e., at the edge of the blind spot). As we discussed earlier, our observed relative predominance of the fellow eye stimulus was consistent with theirs, and consistent with the notion that a stimulus surrounding the blind spot area is a weaker stimulus in rivalry (Baek et al., 2012). However, unlike their analysis, ours focused on the hybrid percept, and our conclusions based on this percept are not consistent with their assertion that filled-in information at the blind spot rivals with the stimulus from the other eye. One possible factor is the earlier authors' assumption that the physical stimulus difference between their ON blind spot ring and disc conditions was negligible, prompting them to attribute differences they observed in perceptual dominance to a filled-in surface in the disc condition. However, it is possible that the physical difference outlined above played a role in bringing about those differences (e.g., their disc stimulus provided more retinal stimulation in the area just outside the edge of the blind spot).

Our findings are consistent with a study about the functional order of phantom filling-in and binocular rivalry. Phantom filling-in is usually induced by two vertical low contrast gratings separated vertically and moving in the horizontal direction (Meng, Remus, & Tong, 2005). When the phantom filling-in inducers were presented monocularly, in conflict with rival stimuli in the other eye, it was found that phantom filling-in only occurred after the inducers became perceptually dominant (Meng, Ferneyhough, & Tong, 2007), indicating the necessity of being aware of the inducers for filling-in to occur. In the context of our present question, their findings suggest that binocular rivalry functionally precedes phantom filling-in, as otherwise phantom filling-in should take place irrespective of whether observers are aware of the inducers or not. Our conclusion of binocular rivalry preceding blind spot filling-in is thus consistent with this study but adds to it, considering that blind spot filling-in is a different phenomenon than phantom filling-in, and is presumably more robust and automatic given that it does not require special stimuli and that it is a common occurrence in situations outside the lab.

Another study that investigated blind spot filling-in in conjunction with a different type of rivalry that does not rely on interocular conflict, found that such monocular rivalry does happen (Chen, Maus, Whitney, & Denison, 2017). Those authors proposed two possible explanations: either blind spot filling-in precedes monocular rivalry between the filled-in representation ("local rivalry" in their terms), or their results actually concern monocular rivalry, acting across a larger retinotopic distance, between the inducer stimuli that they placed near the blind spot ("global rivalry" in their terms). In this latter case, only the perceptually dominant inducer would give rise to filling-in, after perceptual dominance has already been established. To the extent that monocular rivalry and binocular rivalry rely on similar mechanisms (O'Shea, Parker, La Rooy, & Alais, 2009), our findings favor the latter, global rivalry explanation.

In neural terms, blind spot filling-in provides a reference point in the sense that previous studies have demonstrated that its neural substrate lies in V1 (Awater et al., 2005; Júnior et al., 1992; Komatsu, 2006; Matsumoto & Komatsu, 2005). As such, we interpret our results that binocular rivalry functionally precedes blind spot filling-in as support for the notion that early visual areas, including V1 or LGN, may be involved in resolving binocular conflicts. This is consistent with previous research that found fMRI BOLD correlates of binocular rivalry dominance in V1 (Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001) and LGN (Haynes et al., 2005; Wunderlich et al., 2005), and also findings of a reduction, due to rivalry suppression, of aftereffects thought to originate at early visual processing stages (Blake, Tadin, Sobel, Raissian, & Chong, 2006; Gilroy & Blake, 2005). The current study thus suggests LGN as the earliest possible stage that resolves eye-specific conflicts. Interestingly, by assessing the functional order of suppression mechanisms, Breitmeyer (2015) suggested a hierarchy of unconscious processing with binocular rivalry at the lowest/earliest level. Our results, based on the combination of binocular rivalry with a generating mechanism, i.e., blind spot filling-in, are consistent with this general conclusion.

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