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Filling-in at the natural blind spot contributes to binocular rivalry

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Abstract

The human natural blind spot is usually filled in based on the contextual information. When two sufficiently different images are presented to the two eyes, observers typically perceive an alternation between the two images (binocular rivalry). Both the filling-in process and binocular rivalry have been the subject of considerable research. This study investigates whether filled information in one eye's natural blind spot can contribute to binocular rivalry. A radial grating ($D = 12°$) was presented to one eye, centered on the natural blind spot. Observers perceived a complete figure in monocular view; the blind spot area was filled-in based on the surrounding information. Simultaneously, a circular grating smaller than the blind spot ($D = 4°$), was presented to the fellow eye in the region corresponding to the other eye's blind spot. The amount of rivalry as indexed by how often the smaller circular grating remained visible was measured. The results suggest that the filled information in the area of the blind spot does contribute to the rivalry process. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Filling-in; Binocular rivalry; Blind spot

1. Introduction

All humans have a blind spot in each eye's view. It is the area of the visual space that corresponds to the area on the retina where axons of the ganglion cells exit the retina and no photoreceptors are present to receive any visual information. The blind spot is centered about 15° from the fovea on the temporal side of visual space and is about 5° in diameter. The same area for one eye's blind spot in space is covered by the normal intact retina in the fellow eye. For this reason, humans have a complete representation of the whole visual field when both eyes are open. However, even when one eye is closed, one does not see a hole in the visual field. This phenomenon is called 'filling-in' of the blind spot (Ramachandran, 1992a). Exactly what happens at the neuronal level during the filling-in process has been and still is the subject of debate of visual scientists and philosophers alike (Dennett, 1991; Churchland & Ramachandran, 1994). The main dispute is in the active/passive nature of the filling-in process. Those supporting passive filling in hold that the blind spot is simply ignored, just as unseen areas behind the head are ignored. In contrast, those in support of active filling in hold that in the blind spot, a representation is constructed based on the visual stimulation of the area surrounding the blind spot. There is evidence supporting the active nature of the filling-in process (Ramachandran, 1992a,b). In this paper, the filling-in process is combined with another visual phenomenon and the active/passive dispute is put into a direct test by measuringing whether information in the blind spot area of one eye can compete with the information in the corresponding area of the fellow eye.

The two eyes are usually focused at the same point in visual space. Slight differences in viewing angle between the two eyes give stereo disparity information and enhance depth perception. However, the two eyes seldom look at completely different objects. When they do, an interesting phenomenon occurs. As described by DuTour in 1761 of the visual experience when a prism

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was placed in front of one of his eyes resulting in different objects projected to his two eyes: "sometimes I would see only objects projected in the bare eye, sometimes only those in the eye covered by the prism, and sometimes the object projected in one would seem to intermingle with the objects projected in the other." (O'Shea, 1999). This visual phenomenon is termed binocular rivalry. Although the properties of binocular rivalry are a subject of extensive studies (Breese, 1909; Fox & Herrmann, 1967; Wolfe, 1986; O'Shea, 1987; Blake, 1989; Logothetis, Leopold, & Sheinberg, 1996; Lumer, Friston, & Rees, 1998), the neural site responsible for it is still under considerable debate (Lee & Blake, 1999). The experiments described in this paper will at least suggest/constrain the relative sequence of the filling-in and rivalry process.

According to Blake (1989), the reason that one experiences binocular rivalry is that there is conflicting information from two eyes in the same visual area. By definition, there is no binocular rivalry if one eye's information has no competition from the other eye. This makes it possible to examine the nature of the filled information in the blind spot. The vision of someone who is congenitally blind in one eye would be completely based on the remaining eye. Binocular rivalry would not be possible in this case. It is not unreasonable to consider one eye's blind spot as an essentially congenitally blind area. As a consequence, one would not expect to experience binocular rivalry in the region corresponding to the blind spot. However, unlike true congenital blindness, one does 'see' in the blind spot area, due to filling-in. What is the information that one 'sees' at the blind spot area? Can the filled information compete with the real visual input from the other eye? An ignored (non-existent) area should have no power to compete against an input that results from direct stimulation by light. If the blind spot is simply ignored, one would predict that a target smaller than the blind spot presented to the corresponding area in the fellow eye would have no competition. If the blind spot is actively filled-in, one would predict that the smaller target presented to the fellow eye would have to compete with the filled information in the blind spot area, especially if the filling-in process happens at a stage prior to the neural site of binocular rivalry.

The nature of lateral interactions around the blind spot has been studied in an identification task. Tripathy and Levi (1994) found that flankers presented around the blind spot can interfere with the discrimination of a target presented to the position in the other eye that corresponds to the blind spot of the flanked eye. This inter-ocular transfer of the lateral interference around the blind spot suggests that the contextual information around the blind spot area of one eye can influence the detection of a target presented to the fellow eye in the position corresponding to the blind spot. However, their result does not predict whether rivalry will be enhanced by filling-in or not.

In an experiment by Murakami (1995), interocular transfer of motion aftereffect was observed in the blind spot area when the adapting motion was filled-in motion. Prolonged observation of a filled-in motion including the blind spot of one eye could cause a motion aftereffect at the corresponding visual field of the other eye. Based on this result, the author suggested that motion filling-in occurs at an early stage of the visual system.

It remains an open question whether filling-in at the blind spot will support binocular rivalry. The contribution of filled visual information to the process of binocular rivalry was measured. The basic results show that the perceptually filled blind spot does participate in binocular rivalry.

2. Methods

2.1. Observers

Five observers, including the two authors, participated in this experiment. All had normal or corrected-to normal visual acuity. No formal stereo test was administered but all observers could see the image in random dot stereograms. The experiments were performed under the approval of the University of Minnesota human subjects review committee.

2.2. Apparatus

Stimuli were generated with Vision Shell software (http://www.mlink.net/ ~ ml/) running on PowerPC computers. Two Sony 17seII monitors were used to present the stimulus for the left and right eye respectively. The two monitors were positioned 17.5 in. apart, with their viewing screens facing each other. Two mirrors at 90° angle placed in front of the observer brought the stimuli into observers' view (see Fig. 1). Observers' head/eye position was fixed with the help of a chin-rest. Observers' responses were recorded with keyboard presses.

2.3. Stimuli

The basic design of the experiment was to present a rival pair of stimuli to the two eyes. The stimulus for the right eye was a red concentric ring pattern with a 2° outer radius consisting of 3 cycles of square-wave modulation. This stimulus was stationary and had a space average luminance of 5 cd/m^2. For the left eye, the stimulus was a green radial grating, with an outer radius of 12° consisting of 8 cycles of sine-wave modulation. Since a moving stimulus is more powerful in binocular rivalry (Breese, 1909), to enhance the suppression effect of the left eye's large stimulus, it was set in rotation. This stimulus rotated at a rate of 0.1 revolutions/s and had a space average luminance of 16 cd/m^2. In all the conditions, the background was black and the fixation point was a white dot. The fixation point and stimuli were always presented with a rectangular frame (identical in both eyes) to help observers keep their vergence. The vergence was further monitored by Nonius lines that were placed next to the left and right fixation points. As described below, there were six experimental conditions divided into three blind spot conditions and three conditions off of the blind spot. For the blind spot conditions, the positions of the stimuli were adjusted for individual observers, so that they were well centered on the left eye's blind spot. In the off blind spot conditions, the stimuli were moved away from the blind spot to the lower visual field while keeping the eccentricity the same in all conditions (Fig. 2).

2.4. Experimental conditions

The critical measure in this experiment was the effectiveness of the filled information in binocular rivalry. The visibility of the small red target presented to the right eye was used as the index of the suppressing effect from the stimulus presented to the left eye. A total of six conditions were tested (see Fig. 2). They can be classified as

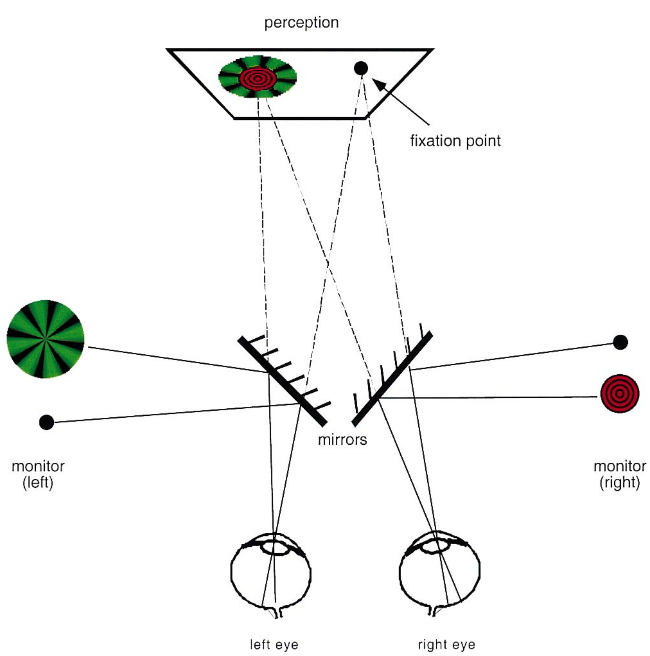

Fig. 1. Schematic diagram of the experimental setup. In this example, the stimuli were centered on the left eye's blind spot. During the experiment, observers usually experience rivalry between the green radial grating and the red circular grating. Their task was to track and record the appearance and disappearance of right eye's small red target.

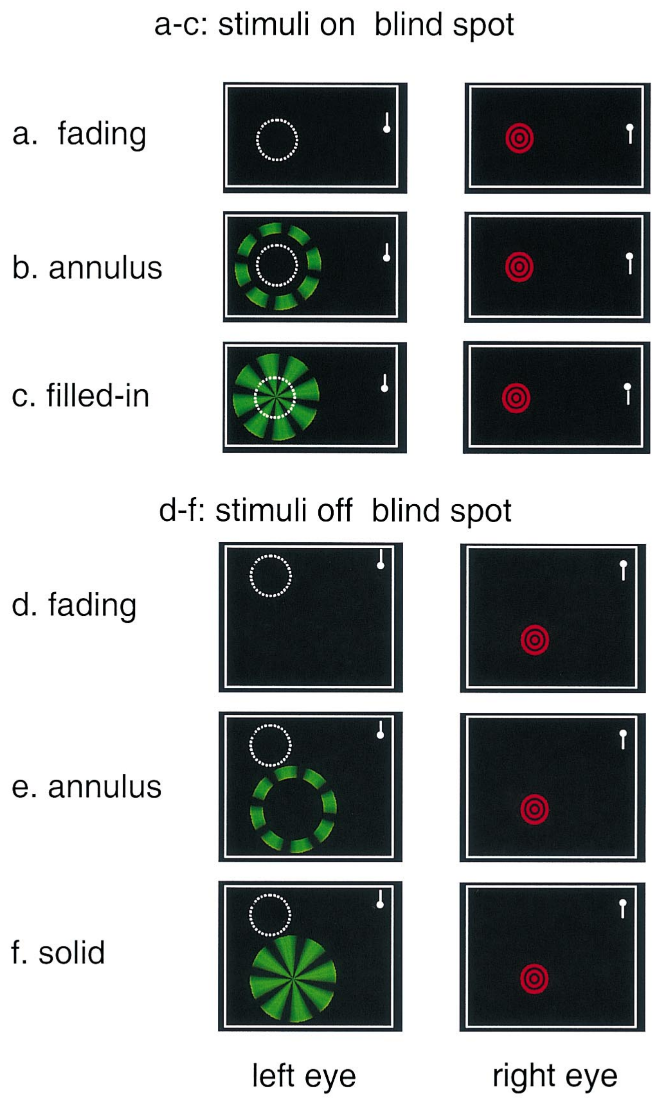

Fig. 2. Six experimental conditions. The white dashed circle in each panel represent the blind spot area of the left eye, no receptors are present on the retina corresponding to this area. (a) Fading condition: no stimulus was presented to the left eye in the fading condition. (b) Annulus condition: a circular area larger than the blind spot (4.5° radius) was removed from the center of the left eye's stimulus, resulting the perception of (a) annulus. Very little or no filling-in occurred. (c) Filled-in condition: stimuli centered on and covered the left eye's blind spot. Observers perceived a complete radial pattern in the left eye due to the filling-in process. Conditions (d) through (f) are similar to (a) through (c), except that the stimuli were moved away from the blind spot to a lower position with equal eccentricity. In all the conditions above, the alignment between the two eyes stimuli was aided with the identical rectangular frames enclosing the two eyes' stimuli and the Nonius lines next to the two fixation points.

three types of stimuli placed in two retinal positions. The two retinal positions were: (1) blind spot — both the left and right eyes' stimuli were presented to the spatial location centered on the left eye's blind spot; and (2) off blind spot — both eyes' stimuli were presented to an area underneath the left eye's blind spot but at the same retinal eccentricity.

The three types of stimuli are: (1) Fading — only the right eye's stimulus was presented. The left eye was presented with fixation point and the frame, but no radial grating. (2) Annulus — the left eye was presented with an annulus, with the inner radius of 4.5°. (3) Solid/filled — the left eye viewed a solid radial grating (off the blind spot) or a filled radial grating (on blind spot). In all conditions, the right eye's stimuli were the same small red circular grating.

In the 'fading' condition, no competing stimulus was presented to the left eye, so this condition measured the spontaneous fading (Troxler effect) of the right eye's small red target. Since different retinal areas may have different sensitivities, with relatively higher sensitivity for one eye's retinal area corresponding to the fellow eye's blind spot, different amounts of fading in the two retinal positions were expected.

In the 'annulus' condition, the left eye's stimulus was an annulus, with an inner radius larger than the radius of the blind spot. When the stimulus was centered on the left eye's blind spot, it created an annulus around the blind spot, with little or no filling-in. The small target in the right eye appeared in the empty center of this annulus. In both retinal locations (on and off blind spot), this measured the visibility of the small target in the presence of inter-ocular lateral suppression coming from the other eye.

In the 'solid/filled' condition, the left eye's large stimulus was a complete radial grating. When it was placed off the blind spot, it measured the regular binocular rivalry between the two figures. When the radial grating was centered on the blind spot, the blind spot was perceptually filled in. The critical question was whether the filled information was just as effective as the real information.

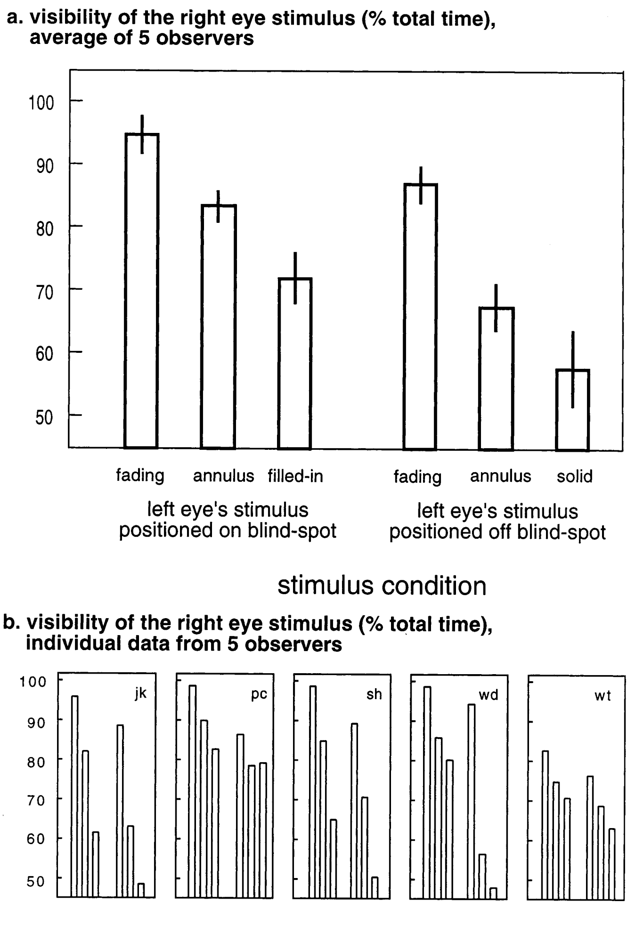

Fig. 3. Results showing the proportion of time that the right eye's small target remained visible. (a) Data are averages from five observers. Error bars are ± S.E.M.s. (b) Individual observers' results. Although each individual had quite different settings, the pattern of results is very similar across observers.

2.5. Procedure

Each observer was first positioned on the chin rest and the boundaries of her/his blind spot of the left eye was carefully mapped using a small moving light spot. Each observer was presented with the stimuli with the configurations discussed above. The presentation of the experimental conditions were randomized for each participant. Each test trial lasted for 2 min. During each trial, the observer tracked the dominant and suppressed phases of the small, red stimulus with key presses of the numeric keypad on a standard keyboard. Pressing the '1' key indicated that the small, red stimulus was not visible (suppressed) and the '3' key meant that the small, red stimulus was visible (dominant). Each observer completed a total of 30 2-min runs consisting of five trials of each of the experimental conditions.

3. Results

The perceptual experience of binocular rivalry is not always a pure alternation between the two eyes' views, particularly when the targets are large. Therefore, in this study the visibility of the smaller target was used as an index for how much rivalry existed. The longer the right eye's smaller target remained visible, the less effective the left eye's competition was. The duration that the small red target remained visible was calculated as the percentage of the total two minutes duration of each trial. For example, if the small target was visible for 60 s, the score would be $60/120 = 0.5$ or 50%.

Fig. 3 shows the averaged results from five observers as well as their individual results. Although each individual observer's settings differ significantly from others, the pattern of results is quite consistent. What is described below for the averaged results, also applies to individual observers.

There are two aspects that can be seen clearly in the results. The three 'on blind spot' conditions and the three 'off blind spot' conditions look very similar to each other in their trends, but differ in the absolute magnitude. The difference is most likely resulted from the fact that the retina is not a homogeneous sheet of photoreceptors. It was found that the retinal region corresponding to the fellow eye's blind spot is typically more sensitive than other areas of the same eccentricity (Wolf & Gardiner, 1963). This sensitivity difference between the blind spot position and off blind spot position lead to different visibility for the right eye's target in the current experiment. In general, the right eye's target was more visible (i.e. more resistant to fading or suppression) when it was placed in the area corresponding to the fellow eye's blind spot.

Within each retinal location, not surprisingly, the red target remained visible the longest in the 'fading' condition. The small fraction of the time when the small target disappeared in the fading conditions was due to the Troxler effect: the spontaneous fading of a target presented to the periphery when a stable fixation was maintained. The small right eye's target disappeared more frequently in the 'annulus' condition, representing the lateral contribution from the annulus to the rivalry process.

When the stimuli were presented in the 'off the blind spot' position, it is not surprising that even stronger rivalry was observed in the 'solid' condition than in the 'annulus' condition. Since the left eye received complete stimulus information, regular rivalry occurred as expected. It is, however, interesting that in the 'blind spot' position, the 'filled-in' condition resulted in a significant increase in the rivalry suppression to the right eye's target. Paired t-tests show that the difference between the 'annulus' and the 'filled-in' conditions is significant ($P < 0.05$). Based on this pattern of results, the main conclusion is that filled information in the blind spot does indeed contribute to binocular rivalry.

4. Discussion

The goal of the present study is to examine the nature of the information filled-in at the human blind spot. The term rivalry implies that there are two sources of information competing with each other. Something that is ignored should not be able to participate in this competition. Thus, by measuring the participation in binocular rivalry of the filled information at the natural blind spot, one can distinguish the active/passive process of filling-in. The results show that the blind spot of one eye, when filled, had a stronger suppression effect on the corresponding region in the other eye compared to when the blind spot was not filled.

Given that the filled information can participate in binocular rivalry, the simplest interpretation would be that the visual system fills the blind spot based on the contextual information prior to or at the neural site(s) of binocular rivalry. Of course, this experiment alone can not determine in absolute terms the operational sequence between filling-in and binocular rivalry. There have been early attempts in localizing the neural site of binocular rivalry psychophysically (Blake & Fox, 1974). Binocular rivalry is likely a multi-stage process (Logothetis et al., 1996). In V1, there are relatively few neurons whose activity follows the perceptual alternation. However, more and more neurons in the extrastriate areas change their activity with the change of perceptual experience during binocular rivalry (Leopold & Logothetis, 1996; Logothetis et al., 1996; Lumer, 1998; Lumer et al., 1998; Tong, Nakayama, Vaughan, & Kanwisher, 1998). Striate cortex is not a good candidate for the neural substrate of filling-in (but see Tripathy & Levi, 1999), because of the clear segregation of the monocular representation corresponding to the blind spot area. The more plausible neural sites for filling-in would be between the transition from the striate cortex to extra-striate cortex. The results indicate that the filling-in process likely happens at least before the completion of the rivalry process. Otherwise, the filled information would enter the scene too late to affect the rivalry process.

Because of the dissociation between physical stimulus and the perceptual experience that occurs during the rivalry process, the rivalry phenomenon has recently been used as a powerful tool to study the neural correlates of visual awareness (Logothetis et al., 1996; Lumer et al., 1998). In general, the neurons whose activity correlates with the perceptual experience are considered possible candidates for the neural correlate of consciousness (NCC). Rivalry offers the opportunity for a stimulus that is physically present but not perceptually experienced. On the other hand, filling-in offers the opportunity for something that is physically non-existent but still experienced perceptually. These two processes seem to contradict one another, yet they may go hand in hand. By similar logic, neurons that do not exhibit filling-in when perceptual filling-in occurs should not be part of the NCC.

Ramachandran (Ramachandran, 1992b, 1995) and Durgin and his colleagues (Durgin, Tripathy, & Levi, 1995) have proposed that filling-in might be an example of a more general surface completion process. Some studies have shown that as early as in V1, neurons have already shown responses to surfaces and filling-in, even when their receptive fields are compeletely inside the surface boundary (Lamme, 1995; Komatsu, Murakami, & Kinoshita, 1996; Zipser, Lamme, & Schiller, 1996; Lee, Mumford, Romero, & Lamme, 1998). With the current advancement of functional brain imaging tools, it is possible to localize and directly examine the local activity of the natural blind spot area (Tootell, Hadjikhani, Vanduffel, Liu, Mendola, Sereno, & Dale, 1998). It would be interesting to study the neural activity with fMRI in V1 in the blind spot area during rivalry.

Note: In an informal observation, the rivalry process between the rods and cones was measured. Rods are largely missing from the central fovea. As a result, there is a blind spot in the center of gaze under scotopic luminance level. Unlike the natural blind spot, the foveal rod blind spot is not usually filled-in. One does perceive a gap in the center of the visual field under appropriate conditions (Hubel, 1997). This provided another opportunity to test the rivalry in the blind spot area when the blind spot is actually not filled. It was first established that when a rod stimulus was presented in the near periphery in one eye and a photopic stimulus was presented in the same region to the other eye, there was strong rivalry (yes, rods do rival with cones!). Then when the stimulus was moved back to the central fovea, the rod stimulus appeared as an annulus and the small cone stimulus in the other eye appeared in the center of the annulus and was visible continuously. In other words, there was no or very little suppression coming from the unfilled region from the left eye.

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