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Perceptual filling-in from the edge of the blind spot

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Abstract

Looking at the world with one eye, we do not notice a scotoma in the receptor-free area of the visual field where the optic nerve leaves the eye. Rather we perceive the brightness, color, and texture of the adjacent area as if they were actually there. The mechanisms underlying this kind of perceptual filling-in remain controversial. To better understand these processes, we determined the minimum region around the blind spot that needs to be stimulated for filling-in by carefully mapping the blind spot and presenting individually fitted stimulus frames of different width around it. Uniform filling-in was observed with frame widths as narrow as 0.05° visual angle for color and 0.2° for texture. Filling-in was incomplete, when the frame was no longer contiguous with the blind spot border due to an eye movement. These results are consistent with the idea that perceptual filling-in of the blind spot depends on local processes generated at the physiological edge of the cortical representation.

Keywords: Human vision; Blind spot; Filling-in; Visual cortex

1. Introduction

The blind spot in human vision refers to the receptor-free area of the retina where the optic nerve leaves the eye. This part of the visual field, subtending 5° × 7° visual angle and centered about 15° temporally, is perimetrically blind in monocular vision, but is hardly ever "seen" because of normal retinal and cortical representation of the corresponding region in the fellow eye. However, even in monocular vision the blind spot is generally not noticed because of perceptual filling-in of color and texture from the surround (Ramachandran, 1992a; Walls, 1954).

Filling-in of color is observed for another naturally occurring scotoma, the foveal blue scotoma (Magnussen, Spillmann, Stürzel, & Werner, 2001, 2004); and filling-in of color, brightness, and texture also occurs in cases of scotomas caused by retinal lesions (Safran & Landis, 1996; Zur & Ullman, 2003). Similar effects are observed during figural fading due to stimulus stabilization on the retina (Gerrits & Vendrik, 1970) or prolonged steady fixation of a target (Hamburger, Prior, Sarris, and Spillmann, 2006; Krauskopf, 1963; Ramachandran and Gregory, 1991; Spillmann and DeWeerd, 2003) and a number of visual illusions demonstrate that color and brightness generated at contours, invade empty fields under ordinary viewing conditions. Well-known examples are the Craik-O'Brien-Cornsweet illusion (Cornsweet, 1970; Davey, Maddess, & Srinivasan, 1998), the neon-color effect (Bressan, Mingolla, Spillmann, & Watanabe, 1997; Van Tuijl & Leeuwenberg, 1979), the watercolor effect (Pinna, Brelstaff, & Spillmann, 2001), and the moving (Menees, Stürzel, & Spillmann, 2002; Tynan & Sekuler, 1975) and stationary (Gyoba, 1983) phantom illusions. Most current explanations of perceptual filling-in phenomena are based on the idea of an active physiological process, a lateral spreading of information generated at contours (e.g. Gerrits & Vendrik, 1970; Ramachandran, 1992a; Sasaki & Watanabe, 2004; Spillmann & DeWeerd, 2003; Spillmann & Werner, 1996); in the case of the blind spot, completion is assumed to result from a process whereby a representation of the missing information is

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created in the non-stimulated cortical area by signals from the surround. Komatsu (2006) recently proposed a neurophysiological model where signals from oriented contrast-sensitive cells along the edge of the blind spot representation spread across a two-dimensional array of feature sensitive cells and color sensitive surface cells, regenerating the missing information.

The results of psychophysical and neurophysiological experiments are consistent with the idea of active information processing in the cortical region corresponding to a scotoma, when the surround is stimulated. With flickering monochromatic blue backgrounds, Magnussen et al. (2001) observed that the foveal blue-scotoma was visible as a dark spot in the center of the visual field, and in a subsequent paper (Magnussen, Spillmann, Stürzel, & Werner, 2004) these same authors showed that the scotoma was visible as a hole in the rapidly fading negative afterimage of the monochromatic background. Presumably in both cases filling-in was counteracted by creating differential activity at the border between the blue-insensitive scotoma and the blue-sensitive retinal surround. Likewise, several studies have shown that scotomas resulting from lesions to the visual pathway may be made visible on dynamic textured backgrounds (Aulhorn & Kost, 1988; Aulhorn, Schiefer, & Herzau, 1990; Bachmann & Fahle, 2000; Churchland & Ramachandran, 1996). In studies of the blind spot, Tripathy and Levi (1994) found that the detection of a test letter "T", presented monocularly within the area corresponding to the blind spot of the fellow eye, was impaired by presenting flanking masker T's around the blind spot of that eye. Furthermore, Murakami (1995) adapted monocularly the retinal region surrounding the blind spot to a drifting grating, and observed a motion aftereffect in the fellow eye, in the region corresponding to the blind spot of the adapted eye. He and Davis (2001) showed that a large radial grating stimulus, centered on the blind spot, produced binocular rivalry in competition with a small stimulus presented to the corresponding monocular region of the fellow eye.

Similar results were obtained by Tong and Engel (2001), who used functional magnetic resonance imaging (fMRI) and found that the BOLD-response to a stimulus rivaling with a stimulus presented to the blind spot of the contralateral eye was similar to the rivalry response obtained when both stimuli fell on corresponding, but functional retinal loci. More recently, functional imaging experiments by Meng, Remus, and Tong (2005) demonstrated physiological filling-in activity in areas corresponding to moving visual phantoms in visual areas V1 and V2. With single-cell recording in the monkey, DeWeerd, Gattass, Desimone, and Ungerleider (1995) found that when the receptive field was entirely enclosed within a gray square presented on a dynamic noise background, the response of the cell to the artificial scotoma first dropped, but then recovered, indicating neural filling-in; this happened at about the same time when perceptual filling-in occurred also for human observers. This filling-in response was particularly prominent in visual area V3.

Most experiments and demonstrations of perceptual filling-in of natural scotomas, including the blind spot, have used stimuli that covered larger regions of the surround, or extended well into the surround of the blind spot (Andrews & Campbell, 1991; Kawabata, 1983; Magnussen et al., 2001, 2004; Ramachandran, 1992a; Zur & Ullman, 2003), one exception being a brief report by Ramachandran (1992b),who observed that with a distribution of rings in the visual field, the ring covering the blind spot "popped out" in perception as a uniform disk. Thus, it is not known whether the mechanism of filling-in depends upon activity along the physiological edge of the blind spot representation or whether the effect depends upon processes that recruit a wider region of the surround. We here show that filling-in of color and texture depends upon a border region of just a few min of arc of visual angle surrounding the blind spot, consistent with an edge account of perceptual filling-in.

2. Methods

The blind spot was mapped with observers positioned on a chin-and-forehead rest fixating a cross with the left eye; their right eye was covered. The cross was presented straight ahead at a distance of 100 cm while a 21 Phillips 201B monitor was positioned to the left such that the blind spot fell onto the computer screen with fixation of the cross. Four OSRAM L36W/25 universal-white fluorescent tubes produced a room illumination of 95 LUX at eye level. To determine the exact shape and position of the blind spot, subjects slowly moved a dim, red laser point across the monitor while fixating the cross, and the positions where the laser point disappeared or reappeared on the screen where marked by the experimenter. The results for these two criteria were averaged and used as coordinates for blind spot testing. We took approximately 60 values depending on each subject's accuracy. This detailed mapping revealed that the borders of the blind spot might be quite irregular, as illustrated in Fig. 1, and varied somewhat between subjects. Thus individual adjustments of the stimulus conditions were necessary.

Based on each observer's blind spot, stimulus frames were generated on a computer, and displayed on the monitor. To test for filling-in of color, frames were prepared in red (CIE: $X = 0.54$, $Y = 0.32$), green ($X = 0.3$, $Y = 0.56$) and blue ($X = 0.14$, $Y = 0.14$), with their width ranging from 0.05°–0.33° visual angle. Preliminary observations showed that on a black background filling-in was perceived more easily than on a white background for identical contrasts, but opposite polarities, between stimulus frame and background. For the actual experiment, we therefore used a luminance of 35 cd/m^2 for the frame and of 4 cd/m^2 for the background ($C = 0.79$).

To test for filling-in of texture, we used black-and-white square–wave gratings of comparable contrast with a spatial frequency of 2 and 3 c/deg oriented either horizontally or vertically. In addition, we presented white-on-black dot patterns of identical figure-ground contrast with dot sizes of 0.17° and 0.25° and an inter-dot distance equaling dot diameter. The width for these frames ranged from 0.17° to 0.66°; with narrower frame widths, texture was not discernible at this retinal eccentricity and hence no filling-in of pattern could be observed. Examples of stimulus frames drawn to scale are shown in Fig. 1. Texture frames had to be wider than color frames to ensure discriminability of the textures. Discriminability was ascertained by repeatedly and randomly presenting each frame at the same retinal eccentricity as the blind spot and asking subjects to report the kind of texture seen.

Observers were instructed to specify whether filling-in of the blind spot was complete or incomplete. In addition, they were asked to rate the amount of filled-in area in steps of 10%. To prevent Troxler-type fading of the frame, observers covered and uncovered the stimulus periodically with

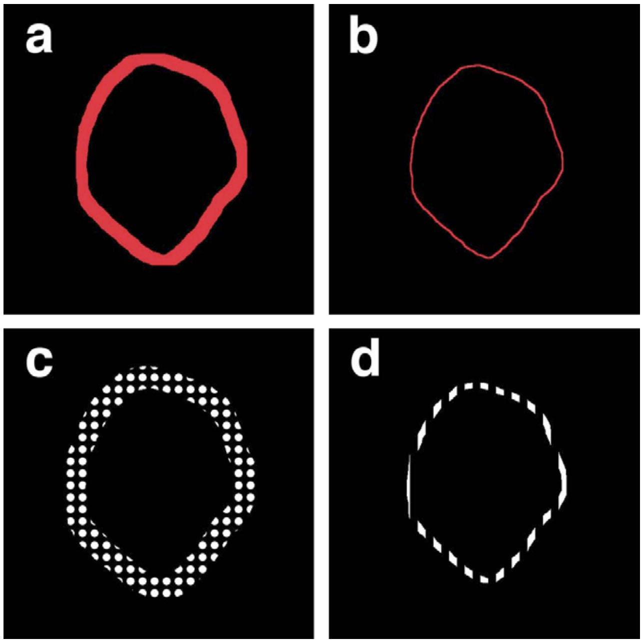

Fig. 1. Examples of individually fitted stimulus frames, drawn to scale. (a) Colored frame of 0.33° width. (b) Colored frame of 0.05° width. (c) Dotted frame of 0.66° width and 0.25° dot diameter. (d) Striped frame of 0.17° width and 2 c/deg spatial frequency.

their hand. On average subjects took 15 s to perform the task, but there was no time limit. Six trained observers (aged between 20 and 30 yrs) with normal or corrected-to-normal visual acuity and normal color vision participated, each completing 12 trials with colored and 18 trials with textured frames. Informed written consent to participate in this study was obtained from all observers.

3. Results

We determined the minimum region around the blind spot that needs to be stimulated for perceptual filling-in by detailed mapping of the blind spot and subsequent placing of individually fitted stimulus frames of different width around the edge. The task was to report all observations pertinent to filling-in of the blind spot.

3.1. Qualitative observations

In the majority of cases observers reported complete filling-in, implying that the color or pattern of the frame perceptually had invaded the blind spot area and filled it uniformly (i.e., 100%), so that it was indistinguishable from the frame. In these cases filling-in was instantaneous, but often lasted less than a second, especially with narrow frames. These short-lived effects may be attributed, in part, to two factors: First, Troxler-type fading which tended to “wash out” the stimulus frame, thereby preventing filling-in of surround properties into the blind spot area; second, involuntary eye movements that displaced the frame relative to the blind spot, thus breaking overall adjacency and resulting in partial filling-in.

In these latter cases, the induced color or pattern still filled most of the blind spot, but left parts of the field empty or foggy. Notably, with improper fixation, one could actually see two dark “shadows“, one on the side where the frame had invaded the blind spot and the other on the opposite side, where the frame had moved away from the blind spot border. Examples of partial filling-in are illustrated in Fig. 2 (a and c) for colored and patterned frames, respectively. To express this aspect of filling-in quantitatively, observers estimated the filled-in area as a percentage of the total.

3.2. Quantitative measurements

Fig. 2 shows the results for the six observers obtained with colored (b) and patterned (d) stimulus frames. The results are presented in terms of the proportion of the blind spot area that was reported as perceptually filled-in. Since we observed no differences between colors, results for red, green, and blue frames were collapsed. Each symbol in Fig. 2b represents the results from one observer (median of the three colors) and the large circles represent the median of the 18 values measured per frame size (6 subjects × 3 colors). The median starts at 80% for a frame width of 0.05°, increasing to nearly 100% with the frame width rising to 0.33°. A closer look at the original data reveals that for colored frames subtending as little as 0.05°, complete (i.e. 100%) filling-in was still observed in 40% of the trials (not shown).

The results for filling-in of texture are similar, except that the data are shifted horizontally towards wider frames (Fig. 2d). Results for dot patterns (collapsed for dot sizes; 6 subjects × 2 dot patterns) are given by orange symbols and for gratings (collapsed for orientation and spatial frequency; 6 subjects × 4 grating patterns) by blue symbols. Filling-in of texture was first observed with a frame width of 0.17°, yielding a median of 70% and 80%, respectively, and rising to nearly 100% when the frame width was 0.33° and 100% when it was 0.66°.

Not surprisingly, perhaps, with a perceptual task of this kind, there are consistent individual differences, with two of the observers having difficulties in observing filling-in with the narrowest frames with both colored and patterned frames.

Curiously, subjects occasionally reported that if the orientation of a grating was difficult to discern when only the stimulus was visible, that orientation became immediately apparent at the moment when filling-in occurred. This implies that the filled-in information induced into the blind spot actually enhanced the percept in analogy to a disrupted line that is seen passing through the blind area (Ramachandran, 1992a). Furthermore, this observation confirms that the smallest frame width used in our experiment was just at the threshold for detection suggesting that the minimum information needed for detection is also the minimum information needed for filling-in.

4. Discussion

The results show that stimulation of a very narrow region immediately bordering the blind spot is sufficient for

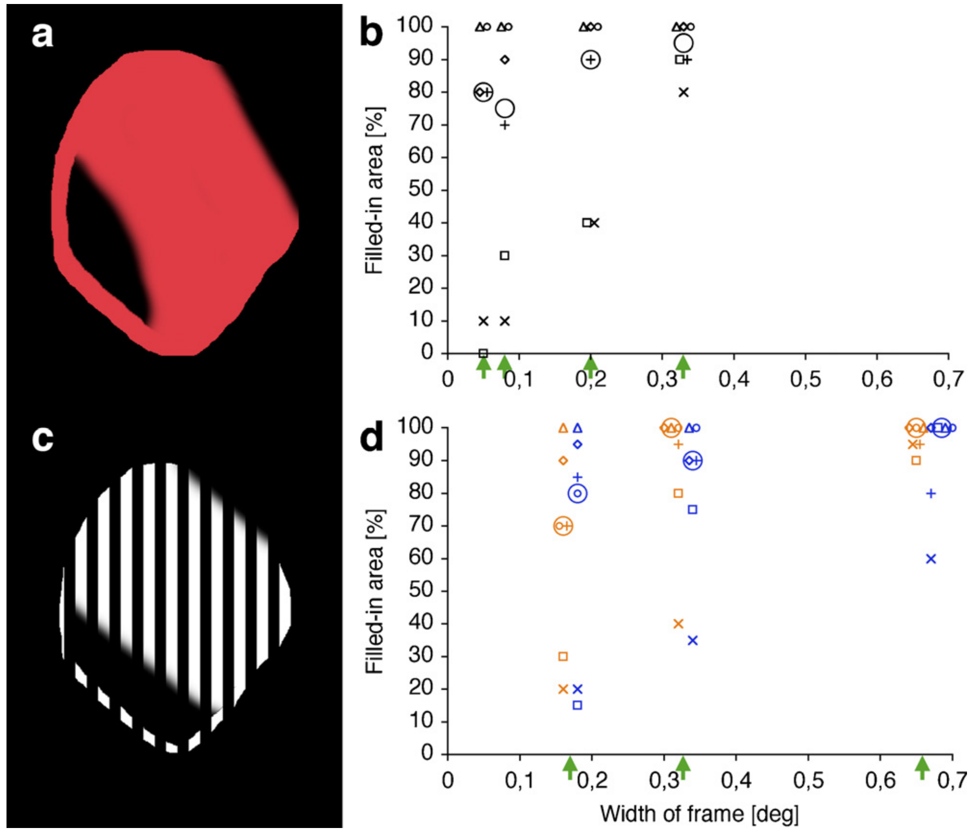

Fig. 2. Qualitative observations and quantitative results on perceptual filling-in of the blind spot. (a and c) illustrate partial filling-in of the blind spot area with either color or texture from the surrounding frame. Panel (b) Area filled-in with color is plotted against width of the surrounding frame. Each symbol represents the data of one subject and gives the median of the results for the tested colors ($n = 3$). The large circles represent the median over all data ($n = 18$) for each frame size. Arrows at the abscissa indicate the tested frame size. (d) Corresponding results are given for perceptual filling-in with dot textures (orange symbols) and gratings (blue symbols); each symbol gives the median of the results of either two sizes of dot patterns or four different grating textures for each subject. The large circles again represent the median over all data ($n = 12$ for dot patterns and $n = 24$ for grating patterns) for each frame size. Note that the dot and grating textures had the same frame sizes but for reasons of clarity we display them slightly shifted. Arrows at the abscissa indicate the tested frame size.

generating perceptual filling-in of color and pattern. During filling-in, the spatial and featural properties of the stimulus frame are preserved, except in the case of partial filling-in, when a dark "shadow" marks the region of the blind spot that is not immediately bordered by the frame (Fig. 2a and d). This partial filling-in effect is theoretically significant inasmuch as it suggests that filling-in is indeed caused by an active physiological process that originates from local stimulation (the surrounding frame) and may be perturbed by local stimulus changes (e.g., lack of adjacency). The results strongly suggest that filling-in depends upon physiological processes generated at a narrow region at the physiological edge of the blind spot representation. Whether signals from retinal regions beyond this physiological edge are ineffective or contribute to the filling-in phenomenon by modifying the border activity, we cannot decide form these experiments.

In general, the results are consistent with the recent model of Komatsu (2006), assuming a lateral spread of signals from oriented contrast sensitive cells along the edge of the cortical representation of the blind-spot region. Evidence for such a process under conditions producing filling-in of artificial scotomas, has been demonstrated in areas V2 and V3 of the monkey visual cortex (DeWeerd et al., 1995). However, in contrast to the gradual climbing activity in that experiment, perceptual filling-in of the blind spot is instantaneous, possibly because the filling-in process is not opposed by border signals from the area to be filled-in as is the case for an artificial scotoma.

An additional contribution to filling-in of the blind-spot may come from binocularly activated color and pattern-specific neurons whose receptive fields cover the area of the monocular blind spot, but extend beyond its borders; such neurons have been described in cortical areas V1 of the monkey (Fiorani, Rosa, Gattass, & Rocha-Miranda, 1992; Komatsu, Kinoshita, & Murakami, 2002; Matsumoto & Komatsu, 2005). This mechanism might explain filling-in of color and grating patterns, but has difficulties with the filling-in of dot patterns, since no feature detectors have been reported for dotted textures.

The idea has been tested that filling-in of the blind spot, rather than being caused by an active physiological process, is the result of passive physiological re-mapping whereby the "hole" corresponding to the blind spot is "sewn up" so that adjacent points in the cortex receive inputs from opposite sides of the blind spot (Awater, Kerlin, Evan, & Tong, 2005; Tripathy, Levi, & Ogmen, 1996). This hypothesis is not supported by either the psychophysical or brain imaging (fMRI) experiments. Awater et al. (2005), probing the cortical regions of the blind-spot surround and the corresponding monocular region of the contralateral eye, found no evidence for a spatial distortion of the physiological activity map of the ipsilateral eye, as would be expected on account of a changed topology in the cortex. Our finding that during perceptual filling-in the area defined by the stimulus frames was invaded by color and texture with no obvious perceptual spatial distortion also speaks against the passive remapping hypothesis.

Hsieh and Tse (2006) have recently conducted an experiment on color mixing during perceptual fading produced by steady fixation, with background and target stimuli of different color, and found that color perception during fading might be a mixture of target and background, but that "forbidden" colors (e.g. a reddish–green) were never observed. In supplementary observations we tested filling-in of color with half the frame in green and the other half in red. In agreement with the observations by Hsieh and Tse (2006) a forbidden color was not observed in this condition, rather filling-in appeared as a bi-partite red–green field with fuzzy borders. Thus, there is no anomalous color mixing in the blind spot area.

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