

# Is neural filling-in necessary to explain the perceptual completion of motion and depth information?

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Retinal activity is the first stage of visual perception. Retinal sampling is non-uniform and not continuous, yet visual experience is not characterized by holes and discontinuities in the world. How does the brain achieve this perceptual completion? Fifty years ago, it was suggested that visual perception involves a two-stage process of (i) edge detection followed by (ii) neural filling-in of surface properties. We examine whether this general hypothesis can account for the specific example of perceptual completion of a small target surrounded by dynamic dots (an ‘artificial scotoma’), a phenomenon argued to provide insight into the mechanisms responsible for perception. We degrade the target’s borders using first blur and then depth continuity, and find that border degradation does not influence time to target disappearance. This indicates that important information for the continuity of target perception is conveyed at a coarse spatial scale. We suggest that target disappearance could result from adaptation that is not specific to borders, and question the need to hypothesize an active filling-in process to explain this phenomenon.

**Keywords:** vision; perceptual completion; filling-in; adaptation

## 1. INTRODUCTION

The first stage of visual perception occurs at the retina, a non-uniform sampling array responding to discontinuous spatial and temporal stimulation. The final stage is visual experience, characterized by objects with coherent surfaces, not simply information about the discontinuities in the world. What is the sequence of neural encoding and representation that generates this impression?

Walls (1954) suggested that visual perception involves a two-stage process. First, the visual system detects discontinuities in the spatial and temporal frequency contents of the visual input. Possible mechanisms for the detection of these discontinuities have subsequently been suggested as locating zero-crossings in the second derivative (Marr & Hildreth 1980) or centroids (Watt & Morgan 1983). This information allows visual features to be grouped and segmented into objects. Second, information about object properties (such as colour and texture), gleaned from the discontinuities, is propagated within the representation of the object, producing uniform neural activity that corresponds to the perception. Thus, a table is perceived as having solid surfaces rather than as just wire-frame edges. This hypothesis, used to explain a range of visual illusions, is influential (Gerrits & Vendrik 1970; Grossberg & Mingolla 1985; Todorović 1987; Paradiso & Nakayama 1991; Gove *et al.* 1995; Grossberg 1997; Grossberg *et al.* 1997; Kamitani & Shimojo 1999).

To probe the neural mechanisms underlying object vision, we consider an ‘artificial scotoma’ (Ramachandran & Gregory 1991; Spillmann & Kurtenbach 1992), a visual illusion involving the completion of information by the

brain. Typically, observers steadily view a peripheral uniform grey target within a field of randomly moving dots; after 15 seconds the target perceptually disappears and only randomly moving dots are perceived. De Weerd *et al.* (1998) suggested that the perceptual fading of an ‘artificial scotoma’ can be considered as a delayed form of the perceptual mechanism outlined by Walls (1954). They suggested that initially a border representation is formed between the homogenous grey target and the surrounding random-noise texture, which allows the two areas to be segmented and distinguished. They speculated that there is neural competition between the representation of the target and that of the surrounding texture, but that the presence of the border keeps the representations distinct. Over time, they suggest that neural adaptation weakens the signal that specifies the discontinuity. Eventually, the representation of the discontinuity is so weakened that it cannot prevent the diffusion of the more prevalent representation of the texture. Effectively, the border representation collapses, and the dominant representation (that of the texture) rapidly diffuses within the target area: thus, the dynamic dots fill-in the target area to produce one surface. An important aspect of this theory is the strength of the border between the dynamic noise and the target: the stronger it is, the longer it should take for the representation of the texture to invade the target area.<sup>1</sup>

Our aim was to test the two-stage fading model as applied to the ‘artificial scotoma’ phenomenon. In particular, we were interested in whether the properties of the border itself are critical, as the two-stage theory would predict. We manipulated the properties of the border between a grey target and a dynamic random-dot background, and then measured how long it took for the target to disappear.

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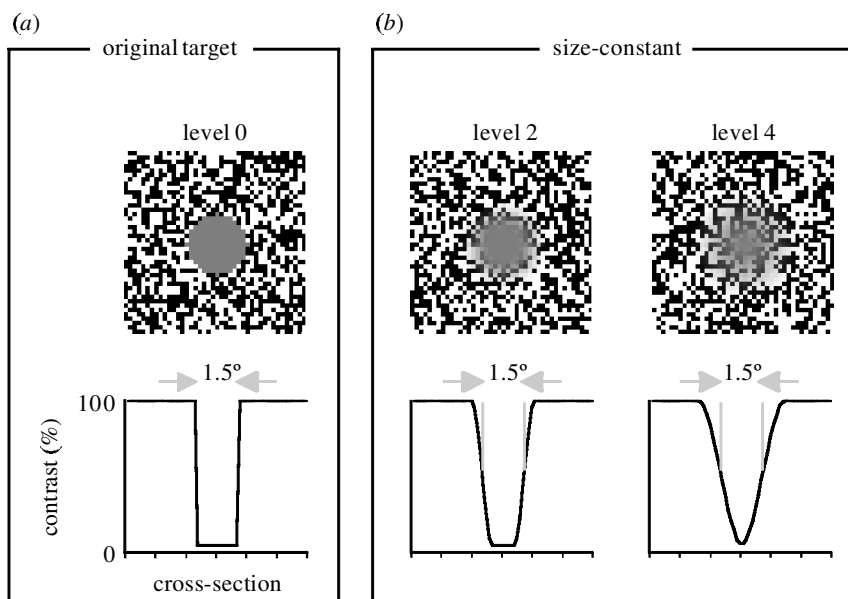


Figure 1. The targets used in experiment one. (a) The original unblurred target and a graph depicting the luminance contrast of the dots for a horizontal cross-section through the centre of the stimulus. In the centre of the target the luminance contrast is zero, whilst in the background texture it is 100%. (b) Examples of targets with different blur levels. Blurring was achieved by varying the spatial extent of a cosine contrast function. The distance between the midpoints of the function was always 1.5°.

## 2. EXPERIMENT ONE: SPATIAL BLUR

Our first manipulation to degrade the borders of the target in the 'artificial scotoma' paradigm was to add spatial blur to the borders. This was achieved by applying a cosine function to the luminance contrast of the dots surrounding the target (see figure 1). Different levels of border blur were achieved by varying the spatial extent of the cosine function. Such a manipulation presents a potential problem. It is known that under the 'artificial scotoma' paradigm increasing the target size increases the time-to-fade (TTF) (Ramachandran & Gregory 1991; De Weerd *et al.* 1998; Welchman & Harris 2001). We needed to ensure that any effects observed when adding blur to the target were not confounded by changes in target size. Previous work on edge detection has supposed that edges are located where there is fastest change in the stimulus luminance (Marr & Hildreth 1980; Watt & Morgan 1983) (i.e. zero-crossings). Therefore, we defined target size as the distance between the midpoints of the cosine contrast functions. Thus, we increased blur by broadening the contrast function whilst keeping the distance between the midpoints constant (see figure 1b). We refer to this condition as size-constant. Assuming that borders (conceived as sharp transitions) are important in the time taken for perceptual completion to occur, the prediction is that more blur (i.e. a lower-spatial-frequency cosine function) should reduce TTF.

### (a) Methods

#### (i) Stimuli

Stimuli were presented on a luminance-calibrated Nanao 17 inch monitor (80 Hz refresh rate; viewing distance 50 cm) controlled by a PC clone containing a number nine Revolution three-dimensional (3D) graphics card. The visual stimulus consisted of the target, a red fixation marker in the centre of the screen and a background filled with a binary random-dot pattern

that was replaced at 20 Hz to generate a white-noise stimulus. Individual dots subtended  $6.6 \text{ arcmin} \times 6.6 \text{ arcmin}$  at the eye. Targets were circular and had a diameter of 1.5°. They were located at 10° lateral eccentricity from the fixation marker. Targets were defined by their difference in luminance contrast from the background (see figure 1). Dots in the middle of the target had 0% luminance contrast (all dots had a luminance of  $51.6 \text{ cd m}^{-2}$ ), whilst the dots in the background had high luminance contrast ( $101.5 \text{ cd m}^{-2}$  dots on a  $1.7 \text{ cd m}^{-2}$  background). Target borders were degraded by applying a clipped cosine contrast function at the edges of the target. Spatial extent of the cosine function was varied by changing its frequency; blur was varied between a maximum of  $0.33 \text{ cycles deg}^{-1}$  (level 4) and a minimum of  $1.33 \text{ cycles deg}^{-1}$  (level 1) in equal steps. Blur step size was around discrimination thresholds obtained elsewhere (Hess *et al.* 1989).

In a separate experiment, we ensured that subjects could discriminate blurred from non-blurred targets to check that the blur steps were perceptually different from one another. Subjects performed a two-alternative forced-choice task. They were presented with a blurred target 10° to one side of the fixation marker, and an unblurred target 10° to the other side. Stimuli were presented for 150 ms, and subjects were required to indicate whether the blurred target was on the left or the right of the fixation point. Fifty data points were obtained for each level of blur, and a discrimination threshold was obtained by analysing the data using probit analysis (Finney 1971). Subject K.J.G. could discriminate all blurred from non-blurred targets, whilst subjects A.E.W. and J.S.M. could discriminate blur level 2, 3 and 4 targets from non-blurred targets.

#### (ii) Procedure

Observers foveated the fixation marker, and pressed a button on a joystick to view the stimulus. They held the button down until the target had faded from view. Once they released the button, a dynamic masking screen appeared for 2 s (for details

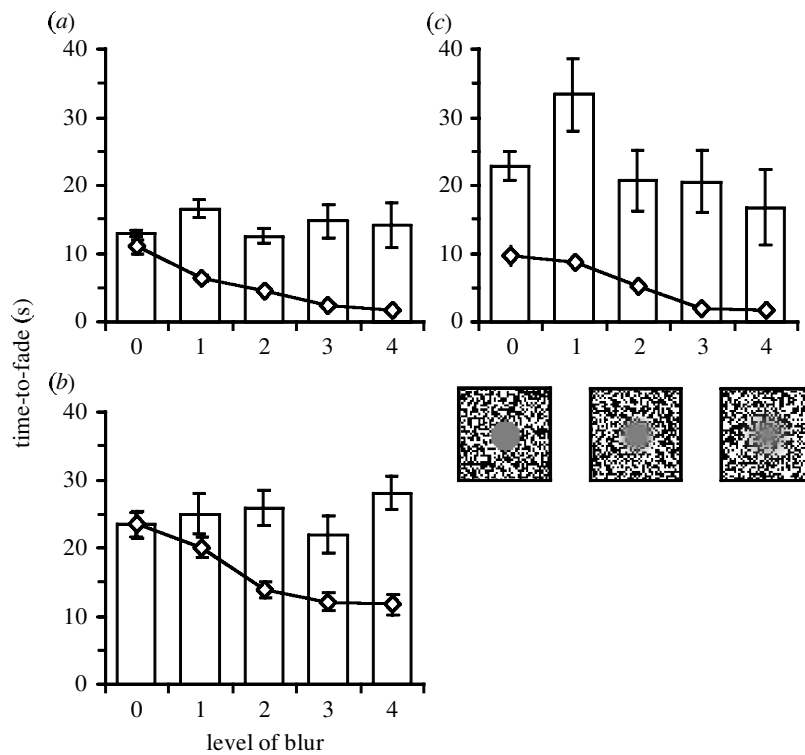


Figure 2. Time-to-fade data plotted as a function of the level of blur for (a) A.E.W., (b) K.J.G. and (c) J.S.M. The bars represent fade times for targets with differing levels of blur. The points connected by lines represent fade times for control stimuli in which the size of the target was made smaller (see § 2b). Error bars represent the standard error of the mean.

see Welchman & Harris (2001)), after which they could initiate the next trial. Different blur levels were interleaved on the same block of trials (one block, 25 trials; one datum, 20 measurements). The mean TTF was calculated for each level of blur.

### (iii) Observers

J.S.M. and K.J.G. were naive to the purposes of the experiments. All observers had normal or corrected-to-normal vision.

### (b) Results

We measured time to fade for three subjects viewing targets with different levels of blur. The data (figure 2a–c, bars) show that TTF is flat as a function of the level of blur. Apart from one point for subject J.S.M., the data are remarkably homogenous. A general linear model confirmed that there were no significant differences between TTFs obtained at different blur levels ( $F_{4,8} = 1.167$ ,  $p = 0.393$ ). This indicates that reducing border clarity does not reduce TTF.

Inspecting the targets presented in figure 1b might suggest that size-constant targets appear to get smaller as blur level is increased. Any effective decrease in size of size-constant targets would be expected to reduce TTF (Ramachandran & Gregory 1991; De Weerd *et al.* 1998; Welchman & Harris 2001). We did not find this: TTF functions were flat, indicating that neither apparent size reductions nor changes in blur affected TTF. To determine the effects of target size, we measured TTF for a range of unblurred targets that were smaller than the original target (target sizes corresponding to the central unblurred portion of the blurred targets). TTF was found to decrease (figure 2a–c, lines;  $F_{4,8} = 31.798$ ,  $p < 0.001$ ),

in line with our expectations. In summary, TTF does not appear to vary as a function of blur.

### 3. EXPERIMENT TWO: DISPARITY BLUR

De Weerd *et al.* (1998) suggested that filling-in mechanisms are employed to effect a coherent surface representation after border adaptation. In experiment one, we found that degrading the borders of a grey target did not affect TTF. In this experiment, we revisited the importance of the borders between the target and the surround, but we adopted a stimulus containing disparity (allowing us to manipulate surface smoothness) to provide deeper insight into the formation of surface representations.

Despite being the traditional stimulus employed in ‘artificial scotoma’ studies, a grey target on a dynamic random-dot background is complex, and it is not obvious that the visual system would treat it as a surface. We approach the notion of surfaces by giving different parts of the stimulus different depths using binocular disparity (cf. He & Nakayama 1992; Nakayama & Shimojo 1992; Nakayama 1996). This approach allows us to manipulate the difference between the target and the background along the single visual dimension of depth, rather than using a stimulus where the target contains both a different luminance contrast and a difference in motion energy. In experiment two, both the target and the background contained a sparse pattern of randomly moving dots. However, dots in the target region had a different disparity from those in the background.

To manipulate border clarity, we varied the continuity of depth in the target and background regions. In some cases, smooth surfaces were used, where all the dots in a

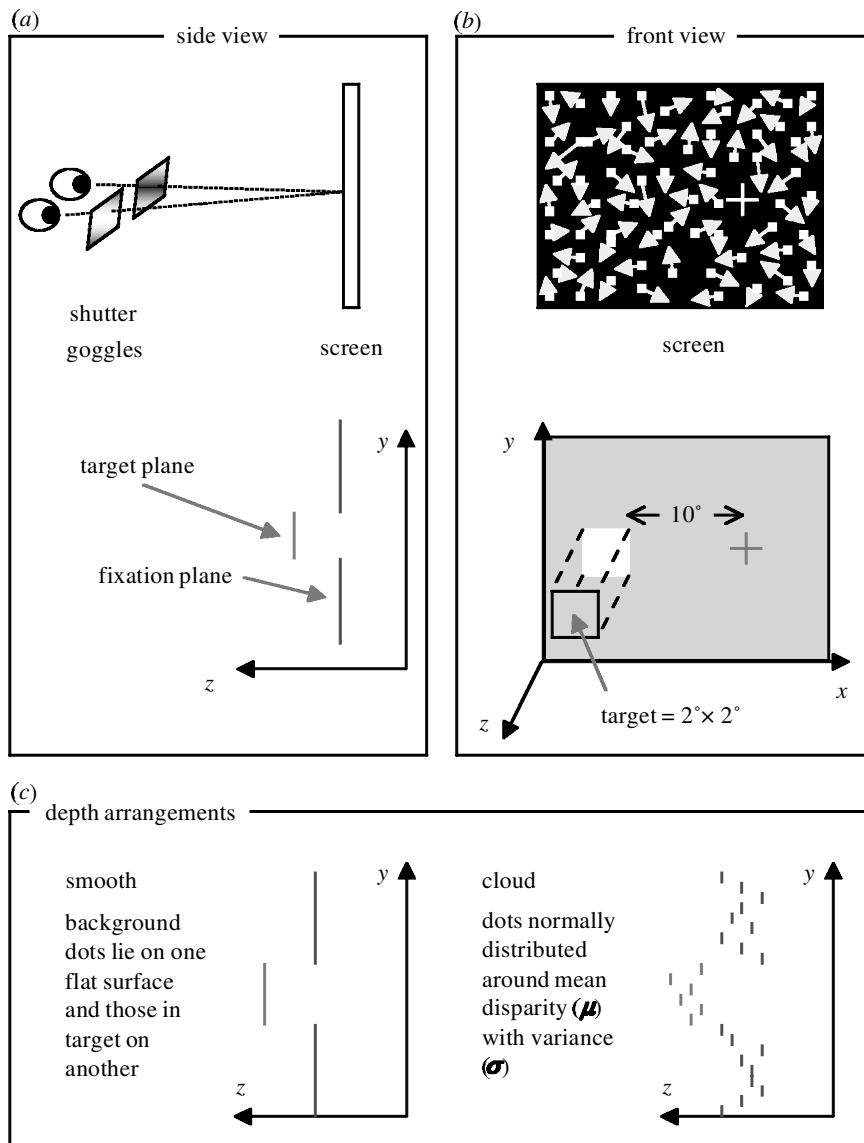


Figure 3. A representation of the set-up used to produce stereoscopically defined stimuli. (a,b) The target area was defined solely by its difference in disparity from the background. (c) A cartoon of the depth arrangements as surface smoothness is varied by changing the distribution of disparities in the stimulus.

stimulus region (target or background) were given disparities corresponding to a single depth plane. In other cases, dots were given a range of different disparities, so that a cloud of different depths was created. This manipulation influences the borders formed between the target and the background regions. In the smooth-plane case, a disparity step-edge is formed between the target and the background, whilst in cloud conditions, disparity edges are random and non-uniform (see figure 3). Assuming that sharp transitions are important, we would predict that well-defined borders should produce long TTFs, whilst degraded borders should adapt quickly, producing short TTFs.

#### (a) Methods

The equipment was that as described above, except that a pair of StereoGraphics CrystalEyes liquid crystal shutter goggles was used to present stereoscopic disparities. The goggles alternated left and right eyes' view of the stimulus at 40 Hz.

#### (i) Stimuli

Both target and background contained a sparse random-dot pattern (5% white dots on a black background). The target was a  $2^\circ \times 2^\circ$  square situated at a lateral eccentricity of  $10^\circ$  from the fixation marker. The pattern of random dots filling the screen changed at 10 Hz to create a dynamic random-noise pattern (higher refresh rates did not support depth perception). The difference between the target and the background was defined solely in terms of the mean disparity of the dots in each region.

Two types of stimulus were examined: smooth, where dynamic dots were located on the same depth plane (variance,  $\sigma = 0$  dots), and cloud, where dynamic dots were distributed ( $\sigma = 1.5$  or 3 dots) across a range of depth planes, forming a spatially random cloud of dots with different disparities (see figure 3c). In the smooth stimulus dots had random two-dimensional motion: target dots moved in random directions in one plane, whilst those in the background moved in random directions in another. In cloud stimuli dots had random 3D motion: the disparity and position of each dot was randomly

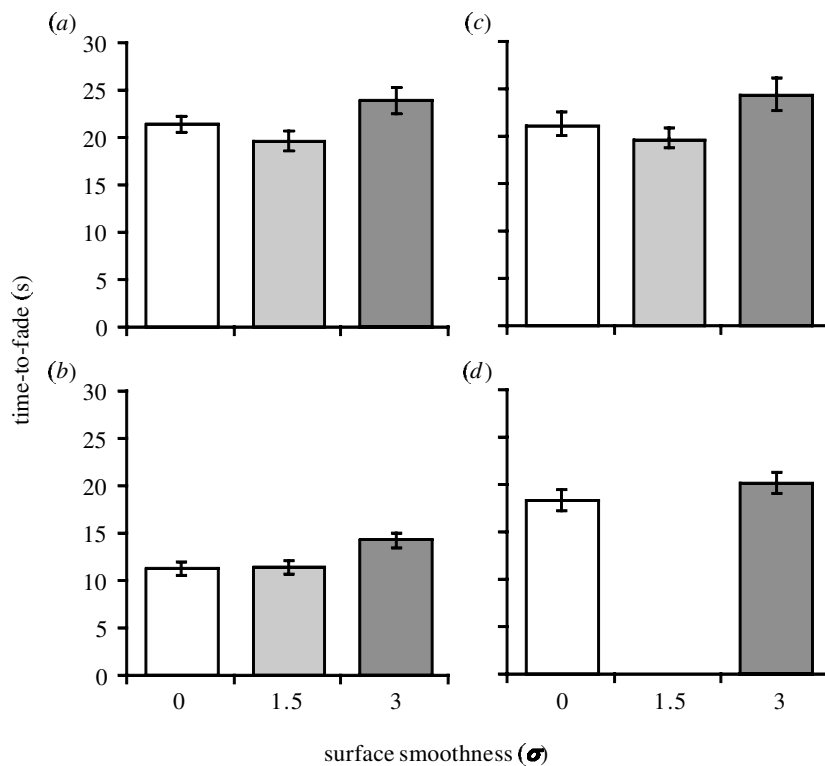


Figure 4. TTF data for (a) A.E.W., (b) K.J.G., (c) V.L.T. and (d) J.M.H., showing the effects of surface smoothness on TTF. Error bars represent the standard error of the mean.

assigned, so that dots formed a cloud of different depths. The difference between the target and the background was defined by the mean disparity in the distributions of dots: background dots were distributed around the plane of the screen, whilst target dots had a crossed or uncrossed mean disparity. Whilst the means of the Gaussian distributions from which disparities were assigned were different for the target and the background, the variances of the distributions were identical.

#### (ii) Procedure

Initial experiments determined the visibility of the targets in each of the smoothness conditions, as the visual system is known to process smooth surfaces more efficiently (Harris & Parker 1994). We measured the mean disparity that observers required to detect the presence of the target using a two-interval forced-choice procedure. Observers were required to indicate the interval in which the target had been presented. Targets were presented at a lateral eccentricity of  $10^\circ$ , and nonius lines were used to promote correct vergence. Presentation intervals lasted 1000 ms and were separated by an inter-stimulus interval of 500 ms. Observers performed at least three runs (one run = seven disparity values  $\times$  20 repetitions = 140 trials) before the data were fit using probit analysis (Finney 1971). Thresholds were obtained separately for each of the three smoothness conditions for both crossed and uncrossed target disparities.

Having obtained detection thresholds for each condition, targets were presented at twice the observers' detection threshold when measuring TTF. This ensured that targets in each condition had the same visibility, and, thus, differences in TTF could not be due to differential visibility of the target. TTF was measured in the same way as described for experiment one. Each experimental run contained 40 trials (20 trials with crossed-disparity targets and 20 trials with uncrossed-disparity targets). The mean TTF was calculated for each level of blur.

Data from crossed and uncrossed mean target disparities were combined for the analysis.

#### (iii) Observers

V.L.T. and K.J.G. were naive to the purposes of the experiments. All observers had normal or corrected-to-normal vision.

#### (b) Results

TTF data for the four observers are presented in figure 4. The data indicate that cloud and smooth conditions produce similar TTFs. The data suggest that cloud ( $\sigma = 3$ ) targets take longer to fade than cloud ( $\sigma = 1.5$ ) or smooth ( $\sigma = 0$ ) targets. This trend is in the opposite direction to the prediction that clear-cut borders should result in longer TTFs than those produced by degraded borders. A general linear model indicated a significant effect of the variance of the disparity distribution ( $F_{2,9} = 32.273$ ,  $p < 0.001$ ). Post-hoc Bonferroni comparisons revealed that the only statistically significant difference was between the  $\sigma = 1.5$  and  $\sigma = 3$  conditions ( $p < 0.001$ ; 95% confidence interval:  $-5.951$  to  $-1.340$ ). These data indicate that cloud targets take as long as, if not longer than, smooth targets to fade. Both experiments one and two indicate that degrading borders has no effect on TTF, and, as such, provides evidence against the role attributed to borders.

## 4. DISCUSSION

#### (a) What is a border?

In this study, we investigated the importance of target borders by degrading the borders through depth continuity and blur. We observed that fading times were not affected by these manipulations, indicating that infor-

mation important for fading is conveyed at low spatial frequencies. The logic of the manipulations we made rests on the assumption that by blurring a target's borders through either spatial extent or disparity continuity we can reduce the border's strength. But, defining a border as the location of zero-crossings will yield a border, however gradual the transition between two regions, provided that the visual filtering mechanisms detecting the discontinuity have a sufficiently large scale. Thus, despite our manipulations, a border representation at the same location will always result. However, the number of detection channels able to respond to the border will vary according to the spatial extent of the blur or the changes in disparity. By blurring the target, fine-scale information is removed, so fewer detectors (only those with coarse scales) will be able to respond to the target's borders, effectively reducing the strength of the border. But, TTF was unaffected in our experiments, indicating that the sharpness of the border is not a critical aspect of the target in the 'artificial scotoma' phenomenon. Therefore, the 'artificial scotoma' phenomenon must use information provided by low spatial frequencies. This in itself is not surprising: to obtain perceptual fading reliably, targets must be presented to the observer's periphery (De Weerd *et al.* 1998; Welchman & Harris 2001), where the low density of retinal sampling (Østerberg 1935) and decreases in the size of cortical projection (Tootell *et al.* 1982) will reduce the amount of high-spatial-frequency information encoded by the brain. However, there is a consequence for our understanding of this phenomenon: if the important information for determining TTF is at low spatial frequencies, then is Walls' (1954) two-stage process necessary to explain the perceptual disappearance of the target?

(i) *Is it a border or a blob?*

If the information important for the long-term visibility of the target is provided by low spatial frequencies, and given that the target is small, are two stages really needed to explain the perception? If the mechanisms that maintain the visibility of the target are spatially extensive, they will be sensitive to the whole region of the target, rather than being especially related to its perimeter. Thus, neurons involved in target perception may be responding to the whole region of the target, rather than specifically to its edges. The implication of this is that if the neurons responding to the target area adapt, there is no need to hypothesize a neural flood of activity following adaptation. If the mechanisms that encode the presence of the target become sufficiently adapted, they will cease to provide a reliable signal specifying a target-background difference. Once the difference signal has been attenuated, the texture appears homogeneous: the visual system does not respond to differences that actually exist in the stimulus. There is no need for a sudden spread of activity to ensure a point-by-point mapping between neurons and perception.

The logic we apply here is reminiscent of the explanation for adaptation provided by Blakemore & Campbell (1969). After adapting to a luminance grating of a particular spatial frequency, observers will require more contrast in the grating to detect its presence than they did prior to adaptation. Blakemore & Campbell suggested that this results from a reduction in the responsiveness of the neural mechanisms encoding spatial frequency. Here, we

suggest a similar notion: changing the response levels of neurons encoding differences in texture or disparity could be responsible for the perceptual completion of an 'artificial scotoma'. (See Anstis (1989) and Durgin *et al.* (1995) for similar suggestions.)

What of the evidence presented by De Weerd *et al.* (1998) for the importance of borders? In one interesting manipulation, they found that displacing the target during the adaptation period prolonged or prevented the completion of the target. As the displacements were small, they suggested that adaptation was occurring at the target's borders. We suggest that displacements of the target delay or prevent adaptation in the population of neurons encoding the presence of the target. Small displacements of the target could change activity in neurons with receptive fields centred in different locations; however, these neurons do not need to respond specifically to high-spatial-frequency information. It could be argued that by comparing the responses of several neurons a high-spatial-frequency border could be signalled (a process known as hyperacuity (Westheimer 1979)); however, these neurons will also be involved in signalling the presence of the target itself.

(b) *Relation to other completion phenomena*

Neural filling-in mechanisms have been proposed to account for a variety of perceptual completion phenomena (e.g. retinal stabilization: Gerrits & Vendrik (1970); the Craik-O'Brien-Cornsweet effect (COCE): Todorović (1987); Grossberg & Todorović (1988); and neon colour spreading: Grossberg & Mingolla (1985); Bressan *et al.* (1997)) and there is psychophysical evidence consistent with the use of filling-in mechanisms in the perception of brightness (Paradiso & Nakayama 1991; Rossi & Paradiso 1996; Paradiso & Hann 1996; Davey *et al.* 1998). How do our data relate to these other phenomena? There are theoretical and empirical reasons why the perceptual completion of an 'artificial scotoma' might be quite different from the filling-in mechanisms underlying brightness perception.

First, 'artificial scotoma' targets are typically presented peripherally, where the mechanisms underlying perception may differ from those used in central visual processing. For instance, psychophysical evidence indicates that in peripheral vision there is an absence of the cellular interactions thought to be responsible for contour linking (Hess & Dakin 1997, 1999). This contour-linking mechanism has been argued to be important in generating the boundaries within which neural filling-in occurs (e.g. Grossberg *et al.* 1997). Other differences between central and peripheral vision, such as reduced contrast sensitivity (Robson & Graham 1981) and increased positional uncertainty (Westheimer 1982), could impact on the use and neural processing of peripheral information. For example, form vision in the periphery has been noted to lack 'distinctness' (Lettvin 1976; Kranda 1998).

Second, the 'artificial scotoma' stimulus is likely to produce very different patterns of neural activity from those produced by, for example, a COCE stimulus. The high-temporal-frequency energy of the random-dot background is likely to preferentially stimulate the magnocellular regions of the geniculate pathway in contrast to the higher parvocellular activity that might be expected for a foveal

COCE stimulus. Further, the areas of cortical activity are likely to differ for the different stimuli. In order for target fading to occur in the 'artificial scotoma' paradigm, temporal energy is necessary (Spillmann & Kurtenbach 1992); this might implicate the necessity of activity in the motion-sensitive middle temporal (MT/V5) area (part of the dorsal processing stream). By contrast, brightness illusions may be more dependent upon activity in the ventral pathway associated with chromaticity and object recognition (DeYoe & Van Essen 1988; Goodale & Milner 1992). The mechanisms implied by models of vision that postulate a role for neural filling-in (e.g. Grossberg 1997) can be associated with activity in the early stages of the ventral pathway (i.e. blob activity in V1; Grossberg & Mingolla 1985).

Third, the theoretical models of vision that postulate neural filling-in (e.g. Grossberg 1997) are principally concerned with the perception of brightness and colour; in these situations filling-in is employed as part of a process of discounting the illuminant, which allows, under normal circumstances, the perception of colours and shades irrespective of the illumination. It has been claimed (Pessoa & Neumann 1998; De Weerd *et al.* 1998) that the same neural filling-in process is involved in the perceptual completion of an 'artificial scotoma'; however, it is not clear why a process postulated to effect brightness perception should be involved in the disappearance of a target in dynamic texture.

Finally, it should be noted that the time-scales of perceptual completion for brightness illusions and the disappearance of an 'artificial scotoma' are very different. De Weerd *et al.* (1998) postulated that the time difference is the result of the time needed for border adaptation. The results of the experiments presented here question the concept of border adaptation. In addition, De Weerd *et al.* (1995) obtained electrophysiological data whilst macaque monkeys viewed an 'artificial scotoma' stimulus. They observed gradual increases in the firing rate (described as 'climbing activity') of some V2 and V3 neurons over a time-course comparable with the monkeys' reports of perceptual completion. It strikes us that this pattern of activity change is more consistent with a gradual reduction in the input to these cells from the target area than it is to a process involving the very rapid diffusion of neural activity after the collapse of a border representation.

## 5. CONCLUSIONS

We have examined the suggestion that the perceptual completion of an 'artificial scotoma' results from the adaptation of a border representation followed by the spread of features from the surround to form a surface. Our data do not support the importance placed on borders. We suggest that it is more pertinent to consider the adaptation of the signals from the whole of the target area. Following sufficient adaptation, perceptual content is no longer determined by a signal that specifies differences between target and background. This explanation does not necessitate a role for rapid neural filling-in to complete an isomorphism between neuronal activity and perception.

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## ENDNOTE

<sup>1</sup>For evidence that increasing the contrast between the target and the surround increases the time to disappearance, see Stürzel & Spillmann (2001) or Welchman & Harris (2001).

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