

A common mechanism for perceptual filling-in and motion-induced blindness [☆]

Li-Chuan Hsu ^{a,*}, Su-Ling Yeh ^{b,*}, Peter Kramer ^b

^a Medical College of the China Medical University, Taichung, Taiwan

^b Department of Psychology, National Taiwan University, Taipei, Taiwan

Received 9 August 2005; received in revised form 31 October 2005

Abstract

Perceptual-filling-in (PFI) and motion-induced-blindness (MIB) are two phenomena of temporary blindness in which, after prolonged viewing, perceptually salient targets repeatedly disappear and reappear, amidst a field of distracters (i.e., non-targets). Past studies have shown that boundary adaptation is important in PFI, and that depth ordering between target and distracter pattern is important in MIB. Here we show that the reverse is also true; that boundary adaptation is important in MIB, and that depth ordering is important in PFI. Results corroborate our earlier conjecture that PFI and MIB are highly related phenomena that share a common underlying mechanism. We argue that this mechanism involves boundary adaptation, but also that the depth effect shows that boundary adaptation can be no more than a sufficient cause of PFI and MIB, and not a necessary one.

© 2005 Elsevier Ltd. All rights reserved.

Keywords: Motion-induced blindness; Perceptual filling-in; Boundary adaptation

1. Introduction

After prolonged viewing, perceptually salient targets can alternately disappear for several seconds, and then reappear again. Two instances of this temporary blindness are perceptual filling-in (PFI) (e.g., Anstis, 1989; Anstis, 1996; Gerrits, De Haan, & Vendrik, 1966; Ramachandran & Gregory, 1991; Ramachandran, Gregory, & Aiken, 1993; Spillmann & Kurtenbach, 1992), and motion-induced blindness (MIB) (Bonneh, Cooperman, & Sagi, 2001). In a typical PFI display (Fig. 1A), a relatively large gray square is presented peripherally on a dynamic noise pattern of black and white random dots. After prolonged viewing, the gray square is perceived to fade, and to give way to the

noise. In a typical MIB display (Fig. 1B), yellow dots are presented on a distracter pattern of coherently rotating blue dots. The blue dots do not enter imaginary rings around the yellow dots. After prolonged viewing, the yellow dots are perceived to fade, but often the imaginary rings around them do not give way to the distracter pattern of blue dots.

After prolonged viewing, distracters are perceived in regions where they are actually not present, both in PFI and in MIB. More liberal definitions of PFI (e.g., De Weerd & Pessoa, 2003; Ramachandran, 2003) consider this the hallmark of PFI, and in that case PFI can be considered to include MIB (and even the Craik-O'Brien-Cornsweet effect; Davey, Maddess, & Srinivasan, 1998). In a more strict definition, a disappearance of a target is required too, but again both PFI and MIB may give rise to that. The difference between the phenomena consists mainly in *what* disappears; whereas in PFI it are especially low contrast and less salient targets that disappear quickly, in MIB—quite counter-intuitively—it are in addition also high contrast and very salient targets. Moreover, whereas in PFI the

[☆] This research was supported by grants from National Science Council of Taiwan (NSC93-2413-H-002-017 and NSC93-2752-H-002-008-PAE).

* Corresponding authors. Tel.: +886 4 22053366x8624; fax: +886 4 22053764 (L.-C. Hsu).

E-mail addresses: lichuanhsu2001@yahoo.com.tw (L.-C. Hsu), suling@ntu.edu.tw (S.-L. Yeh).

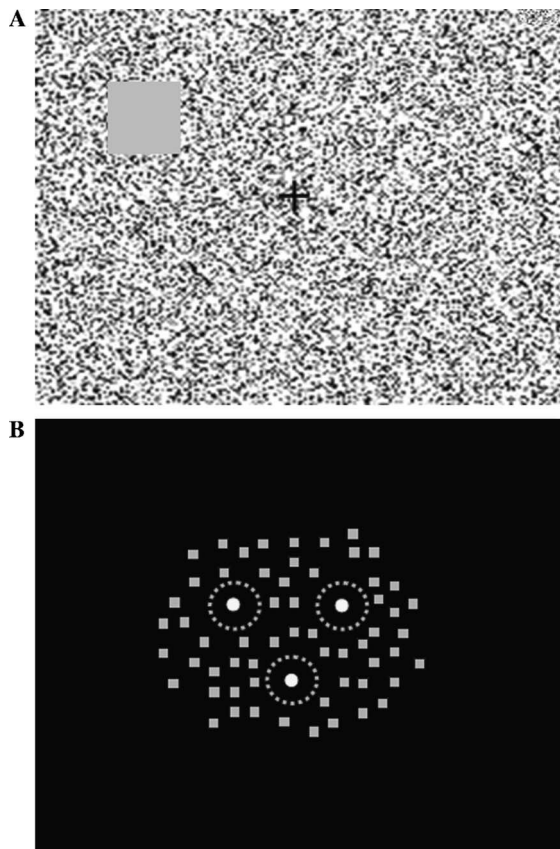


Fig. 1. (A) A typical perceptual filling-in (PFI) display, with a gray square as a target, and high density black and white dots as distractors. (B) A typical motion-induced blindness (MIB) display, with three yellow dots as targets (shown here in white), three non-salient black zones around these targets (here indicated by white dotted lines that were not shown to the participants), and a number of sparsely distributed random dots as distractors (shown here in gray) on a black background. The zones surrounding the targets are not salient when the distractors are stationary, but are slightly more salient when the distractors are moving.

disappearance of targets and subsequent interpolation of the surrounding area appears to be complete, in MIB regions around the targets are spared from interpolation.

The two phenomena have also been attributed to very different causes. Whereas boundary adaptation has been demonstrated to affect PFI, and subsequent interpolation of the distracter pattern is also considered important for it (e.g., De Weerd, Desimone, & Ungerleider, 1998; De Weerd, Gattass, Desimone, & Ungerleider, 1995; Francis, Grossberg, & Mingolla, 1994; Grossberg, 1994; Grossberg & Yazdanbakhsh, 2005; Kelly & Grossberg, 2000; Ramachandran et al., 1993; Spillmann & De Weerd, 2003), the relative order of depth of the target and the distracter pattern has been shown to be important in MIB (Graf, Adams, & Lages, 2002), and there is also some speculation that shifts of attention could be important for it (e.g., Bonneh et al., 2001; Sagi & Gorea, 2003).

The *boundary adaptation effect* that has been demonstrated in PFI, consists in the fading of the boundaries of the target after prolonged viewing, followed by the interpolation of the surrounding distracter pattern that subse-

quently renders the target invisible. Gerrits et al. (1966) suggest that adaptation of boundaries reduces neural inhibition of features spreading across them. De Weerd et al. (1998), taking the cortical magnification estimates into account of Sereno et al. (1995), found that the time course of PFI is linearly related to contour length in the visual cortex, rather than on the retina, and thereby showed that the relevant boundary adaptation must be cortical rather than retinal. These ideas and results have also been taken into account by the computational models of Francis et al. (1994), Grossberg (1994), and Neumann and Mingolla (2001).

The effect of the relative order of depth of the target and the distracter pattern (henceforth called *depth effect*), that has been shown to affect MIB (Graf et al., 2002), is of a completely different nature than the boundary adaptation effect. It consists in the relatively easy fading of the target when it is presented behind the distracter pattern rather than in front of it. Graf et al. (2002) argue that the distracter pattern forms a surface, and that when it completes in front of the target, it forces this target out of view. We do not think the explanation is entirely convincing, because it begs the question why these surfaces must necessarily be seen as opaque (forcing the target out of view), rather than as transparent (leaving it visible). Moreover, Graf et al. also admit that although targets in front are not perceived to disappear as often as targets in back, the former are still perceived to disappear every once in a while. Their experimental result of a robust depth effect, however, is nevertheless quite intriguing, since it cannot be explained by boundary adaptation in any straightforward way.

The boundary adaptation effect in PFI and the depth effect in MIB suggest the involvement of very different mechanisms. Earlier, however, we found that PFI and MIB are similarly increased by eccentricity and reduced by the luminance contrast of the target with a small surrounding area that was kept free of distracters (Hsu, Yeh, & Kramer, 2004). Some high contrasts seemed to increase MIB rather than to decrease it (Bonneh et al., 2001; Hsu et al., 2004). However, those were exactly the contrasts that rendered the luminance of the target least similar to that of the distracters in the distracter pattern. Our subsequent experiments showed that poor perceptual grouping between target and distracters (i.e., good segregation) leads to more MIB than good perceptual grouping (i.e., poor segregation). Hence, the exceptional contrast effects were in all likelihood confounded with effects of perceptual grouping. These results suggest that PFI and MIB are not categorically different phenomena, and that they both share a common underlying mechanism (or perhaps several common underlying mechanisms). However, if this is indeed so, then (1) the *boundary adaptation effect* that has been demonstrated in PFI, should be replicable in MIB, and (2) the *depth effect* that has been shown in MIB, should also be replicable in PFI. In this study, we test both these predictions in a series of four experiments.

In Experiment 1 (MIB), the effect of boundary adaptation was investigated, by pre-adapting stimuli that either overlapped with the boundaries of the target, or that did not. In Experiment 2 (PFI and MIB), and Experiments 3 and 4 (only MIB), the effect of boundary adaptation was investigated again, but now adaptation was manipulated by varying the length of the boundary of the target in several different ways (because the longer the boundary, the slower its adaptation; De Weerd et al., 1998). The boundary was lengthened, by increasing the target's size (Experiment 2), irregularity (Experiment 3), and radial frequency (Experiment 4). Finally, in Experiments 2, 3, and 4, the effect of the depth of the target, relative to the distracter pattern, was also investigated, as well as its possible interaction with the effects of the three different boundary adaptation manipulations.

2. General methods

2.1. Observers

Two naïve but experienced observers, and author LCH, participated in Experiment 1. Three naïve but experienced observers, and LCH, participated in Experiments 2, 3, and 4. All observers had normal or corrected-to-normal vision, and the naïve observers were paid 100 New Taiwan Dollars per hour for their participation.

2.2. Apparatus, stimuli, and design

The stimuli were constructed with, and controlled by, Presentation v0.80 software (Neural Behavior Systems Corporation), using an IBM compatible personal computer with a 17 inch calibrated EIZO color monitor that was viewed from a distance of 50 cm in Experiment 1, and from a distance of 120 cm in Experiments 2, 3, and 4. In these latter experiments, stereoscopic stimuli were used that were fused with the help of an apparatus that revealed identical stimuli to the left and right eyes, except for a variable disparity between their targets. All experiments had completely pseudo-randomized within-subjects designs.

2.3. Procedure

In all experiments, observers were to fixate a small red square in the beginning of each trial. They initiated a trial by pressing the enter-key, and pressed the left-arrow key when the target was perceived to disappear, and the right-arrow key when it was perceived to reappear. The latter two keys were both controlled by the right hand, and the former key (the enter-key) was pressed by a hand of choice. Each trial lasted 30 s in Experiment 1, and 1 min in Experiments 2, 3, and 4. To prevent fatigue, self-paced short breaks were allowed in between trials.

In Experiment 2, 3, and 4, observers were first provided with some practice fusing the stereoscopic stimuli, using classic random-dot stereograms (e.g., Blakemore & Julesz, 1971). Squares consisting of random dots were presented with some disparity amidst other random-dots that had a zero disparity, and the participants had to judge whether these squares appeared in front or behind the other dots. None of the participants had trouble fusing the stereograms. During the experiment proper, several practice trials were performed too, to ensure that the task had been understood properly.

In all experiments, the total perceived fading duration was measured. The elapsed time until the first disappearance of the target (i.e., the "initial fading time") is another common measure of PFI and MIB. However, the initial fusion of the stereoscopic stimuli in Experiments 2, 3, and 4 requires some variable amount of time that complicates interpretation, and for this reason it was not measured here.

3. Experiment 1: Boundary pre-adaptation in MIB

In this experiment, the presentation of an MIB display was preceded by a pre-adaptation display (Fig. 2), in which either square frames of different sizes, or patterns of random dots, were adapted. Pre-adaptation of the frame that exactly fitted the boundary of the target was expected to produce more MIB than pre-adaptation of the other frames. Pre-adaptation of the random dot patterns that covered the area of the target, but did not cover its boundary, was not expected to produce much MIB. Although the number of pixels used to draw the random dot patterns exactly matched the number of pixels used to draw the square frames, the great majority of them did not overlap with the location of the target's boundary. Thus, if the pre-adaptation of these random dot patterns would also

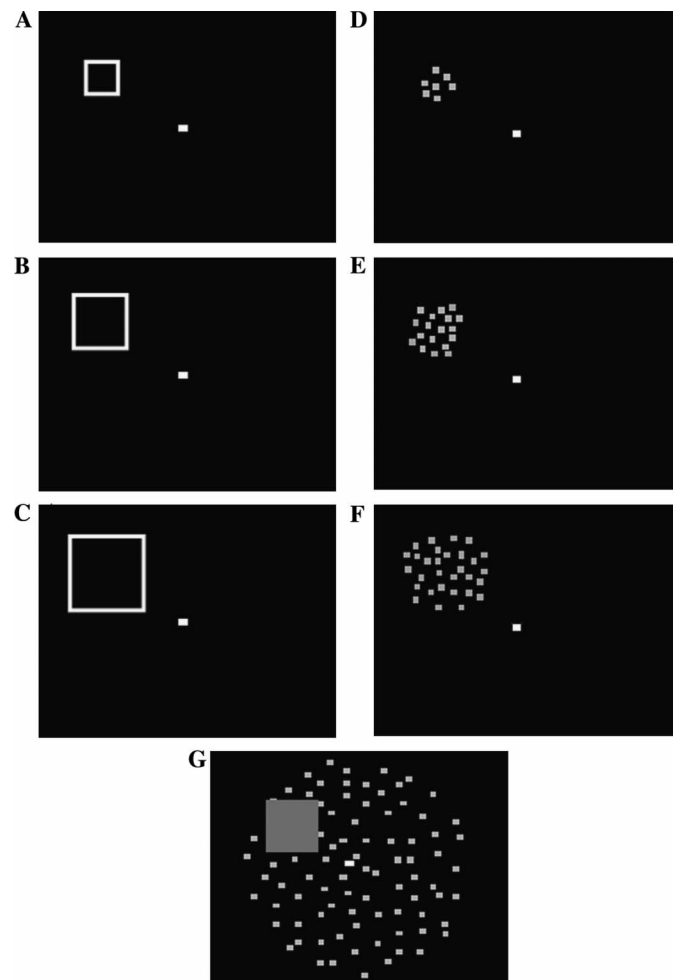


Fig. 2. Stimuli of Experiment 1: (A–F) show stimuli used in the pre-adaptation phase. (G) shows the MIB display with a gray, square target, a red fixation dot (shown here in white), and blue, dynamic, random-dot distracters (shown here as small gray squares). (A–C) show pre-adaptation frames. Frame A is smaller than the boundary of the MIB target, Frame B fits it exactly, and Frame C is too large. (D–F) show pre-adaptation random-dot patterns. Pattern D contains the same number of pixels as Frame A, Pattern E the same number as Frame B, and Pattern F the same number of pixels as Frame C. The patterns also occupy the same area as the frames.

cause MIB, then boundaries could not be considered critical to it.

3.1. Method

3.1.1. Stimuli

The MIB display contained a gray, square target ($2.19^\circ \times 2.19^\circ$ in size, and 5 cd/m^2) on a black background ($.10 \text{ cd/m}^2$). The target was presented with an eccentricity of 8.58° from a red fixation square ($.30^\circ \times .30^\circ$ in size, and 18 cd/m^2 , CIE (0.602, 0.322)). A hundred sparsely distributed (1% density) blue random dots (each $.25^\circ$ in diameter, i.e., 5 pixels) with a luminance of 20 cd/m^2 and a CIE of (.151, .070) served as a distracter pattern. They were contained in an area with a radius of 13.18° , and rotated together, with a speed of .28 revolutions per second, in a clockwise direction. The mean luminance of the background and dots together was $.33 \text{ cd/m}^2$.

The square frames that were used during the pre-adaptation phase were $1.59^\circ \times 1.59^\circ$, $2.19^\circ \times 2.19^\circ$, or $3.08^\circ \times 3.08^\circ$ in size, $.05^\circ$ in width (i.e., 1 pixel), and were gray (2 cd/m^2) on a black background ($.10 \text{ cd/m}^2$). The random dots that were also used during the pre-adaptation phase were each $.05^\circ \times .05^\circ$ in size, and gray (2 cd/m^2) on a black background ($.10 \text{ cd/m}^2$). Thus, the experiment contained six conditions (three square frame conditions, and three random dot conditions), and each condition contained six trials.

3.1.2. Procedure

All trials were each preceded by a pre-adaptation phase that lasted 15 s (about the same as the initial fading duration in a normal PFI task; De Weerd et al., 1995; Ramachandran et al., 1993), in which either one of the square frames, or one of the random-dot patterns was used (Fig. 2).

3.2. Results and discussion

Fig. 3 shows the results. A multivariate analysis of variance (a more conservative alternative to a repeated-measures analysis of variance; see, e.g., Tabachnick & Fidell, 1989) revealed a significant effect of pre-adaptation (Wilk's lambda = .46, $F(1,17) = 19.92$, $p < .001$; univariate $F(1,17) = 19.91$, $p < .001$), a significant effect of the size of the pre-adapted stimulus (Wilk's lambda = .21, $F(2,16) = 29.32$, $p < .001$; univariate $F(2,34) = 44.45$, $p < .001$), and a significant interaction effect between the kind of pre-adaptation, and the size of the pre-adapted stimulus (Wilk's lambda = .36, $F(2,16) = 14.19$, $p < .001$; univariate $F(2,34) = 18.12$, $p < .001$). Within participants, 60% of the variance was due to the experimental manipulations.

The exact proportions of the total presentation durations during which the target was not seen were: 12, 13, and 15% (for, respectively, the small-, medium size-, and large random-dot stimuli), and 13, 22, and 14% (for, respectively, the small-, medium size-, and large frame stimuli). These results corroborate our hypothesis that boundary adapta-

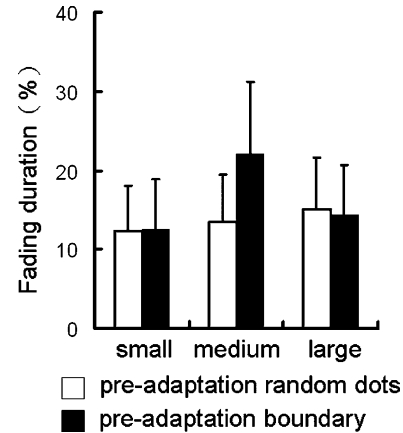


Fig. 3. Results of Experiment 1: the abscissa shows whether the pre-adaptation stimulus was smaller in size than the target, fitted exactly, or was larger. The white bars show the results after pre-adaptation to a random-dot pattern, and the black bars show the results after pre-adaptation to a frame. The ordinate shows the percentage of the total duration that the target was perceived to have disappeared, and the error bars represent 1 standard error.

tion is not only a sufficient cause of PFI, but also of MIB. Only when a frame was pre-adapted, namely, that fitted the boundary of the target exactly, was a significant rise in fading duration observed. Pre-adaptation of a frame that did not fit the boundary, or pre-adaptation of random-dots that covered merely the inside of the target, rather than its boundary, did not produce equally long fading durations.

4. Experiment 2: Target size and depth in PFI and MIB

In this experiment, both PFI and MIB displays were used. The effect of the length of the boundary of the target was investigated, by varying target size. Long boundaries hamper their adaptation, and this leads to less PFI. Here we predicted that they affect MIB in the same way.

4.1. Method

4.1.1. Stimuli

The gray target had an eccentricity of 5.42° from a red fixation square ($.12^\circ \times .12^\circ$ in size, and 18 cd/m^2 , CIE (0.602, 0.322)), and could be either $.31^\circ \times .31^\circ$, $.46^\circ \times .46^\circ$, or $.62^\circ \times .62^\circ$ in size. It had a luminance of 50 cd/m^2 in the PFI displays, and a luminance of 10 cd/m^2 in the MIB displays.

In the PFI displays, the target was presented on a distracter pattern that consisted of densely packed 50% black and 50% white dynamic random dots ($.10$ and 100 cd/m^2 , respectively), that were each $.02^\circ$ in diameter (i.e., 1 pixel). The dots had a random phase, and a temporal frequency of 10 Hz, which has been shown to be optimal for inducing PFI (Spillmann & Kurtenbach, 1992). The area that contained the dots had the shape of a disk with a 3.11° radius. The area outside the disk was gray (50 cd/m^2).

In the MIB displays, the target was presented amidst sparsely distributed blue random dots (with a density of

3%, and each $.06^\circ$ in diameter, 20 cd/m^2 , and with a CIE of $(.151, .070)$ on a black background ($.10 \text{ cd/m}^2$) that covered a disk-shaped area with a radius of 3.11° . These random dots coherently rotated together with a speed of $.28$ revolutions per second. The mean luminance of the background and dots together was $.33 \text{ cd/m}^2$.

The target was presented at one of three different stereoscopic depths, by shifting the target for the right eye to the left by either $.21^\circ$, 0° , or $-.21^\circ$, and hence, the target could appear either in front of the distracter pattern, at about the same depth (ignoring monocular depth cues), or behind it. In total, the experiment contained 18 conditions (PFI vs. MIB display type \times 3 different boundary lengths \times 3 different target disparities). Each condition contained six trials.

4.2. Results and discussion

Fig. 4A shows the results of Experiment 2, when a PFI display was used. A multivariate analysis of variance revealed significant effects of both boundary length (Wilk's lambda = $.68$, $F(2,22) = 5.11$, $p < .05$; univariate $F(2,46) = 7.57$, $p < .001$) and disparity (Wilk's lambda = $.24$, $F(2,22) = 35.24$, $p < .001$; univariate $F(2,46) = 55.36$, $p < .001$). Their interaction was not significant (Wilk's lambda = $.91$, $F(4,20) = .51$, $p > .73$; univariate $F(4,92) = .64$, $p > .64$), although—as will be shown

in a moment—statistical contrasts suggest the boundary length and the depth effects in PFI are not completely independent after all. Within participants, 54% of the variance was due to the experimental manipulations.

Fig. 4B shows the results of Experiment 2, when an MIB display was used. A multivariate analysis of variance revealed significant effects of boundary length (Wilk's lambda = $.33$, $F(2,22) = 21.92$, $p < .001$; univariate $F(2,46) = 29.49$, $p < .001$) and disparity (Wilk's lambda = $.15$, $F(2,22) = 61.44$, $p < .001$; univariate $F(2,46) = 95.58$, $p < .001$), but in addition their interaction was also significant (Wilk's lambda = $.45$, $F(4,20) = 6.24$, $p < .01$; univariate $F(4,92) = 5.94$, $p < .001$). Within participants, 67% of the variance was due to the experimental manipulations.

Contrasts revealed that when the target had a positive or zero disparity, longer boundary lengths led to less PFI and less MIB (when the target had a positive disparity $F(2,138) = 5.27$, $p < .001$ for PFI, and $F(2,138) = 32.61$, $p < .001$ for MIB, and when the target had a zero disparity $F(2,138) = 5.53$, $p < .001$ for PFI, and $F(2,138) = 6.65$, $p < .001$ for MIB). Moreover, when the target had a negative disparity, longer boundary lengths did not lead to less PFI or MIB ($F(2,138) = 1.9$, $p = .09$ for PFI, and $F(2,138) = 1.29$, $p = .29$ for MIB).

Previous studies have shown that large target sizes reduce PFI (e.g., De Weerd et al., 1998; Ramachandran & Gregory, 1991). Our results corroborate this finding (Fig. 4A), but only for targets that are presented with a positive or zero disparity, and not for those that are presented with a negative disparity. Moreover, our results show that large target sizes also reduce MIB (Fig. 4B), and also only for targets that are presented with a positive or zero disparity, and not for those that are presented with a negative disparity.

The results show that boundary length is critical in both PFI and MIB. The longer the boundary, the less it fades, at least when the target is in front or in the same depth plane as the distracter pattern. The depth of the target relative to the distracter pattern is also critical in both PFI and MIB. When the target is presented behind the distracter pattern, it fades much more easily than when it is presented in front of it, or in the same depth plane. Noteworthy is also that the effect of boundary adaptation appears to be stronger when the target is presented in front of or in the same depth plane as the distracter pattern, rather than behind it. This effect appears in the results of the next experiments also, and we will discuss it in Section 7.

5. Experiment 3: Boundary regularity and depth in MIB

In Experiment 2, target boundary length was manipulated by varying target size. In the current experiment, however, to ensure that the important factor is indeed the boundary length of the target, and not its size, boundary length was manipulated while controlling target size.

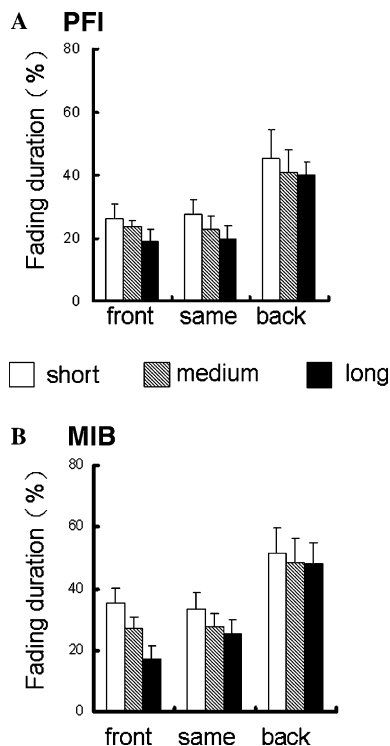


Fig. 4. Results of Experiment 2: (A) shows PFI results, and (B) MIB results. In both cases, the abscissa shows whether the target appeared in front of the distracters, at the same depth, or behind them. The white bars show the results for a target with a short boundary (a small target), the hatched bars the results for a target with a medium long boundary (a medium large target), and the black bars the results for a target with a long boundary (a large target). In both (A) and (B), the ordinate shows the percentage of the total duration that the target was perceived to have disappeared, and in both the error bars represent 1 standard error.

5.1. Method

5.1.1. Stimuli

In this experiment, only an MIB display was used, for which previously boundary adaptation has not been investigated. Boundary length was now manipulated by changing the shape of the target, while keeping its total area constant at $.99^\circ \times .99^\circ$ (Fig. 5). In this way, the length of the boundary could be either 3.98° , 5.47° , or 6.69° long. The size of the target was a bit larger than in Experiment 2, and hence, we also expect somewhat less MIB than in that experiment. We manipulated depth again too, just to be sure no effects of boundary adaptation would be missed in case of an interaction between boundary adaptation effects and depth effects. In other respects, the stimuli looked similar to the MIB stimuli used in Experiment 2 as well. In total, the experiment contained 9 conditions (3 different boundary lengths \times 3 different target disparities), and each condition contained six trials.

5.2. Results and discussion

Fig. 6 shows the results. A multivariate analysis of variance revealed significant effects of boundary length (Wilk's lambda = .71, $F(2,22) = 4.53$, $p < .05$; univariate $F(2,46) =$

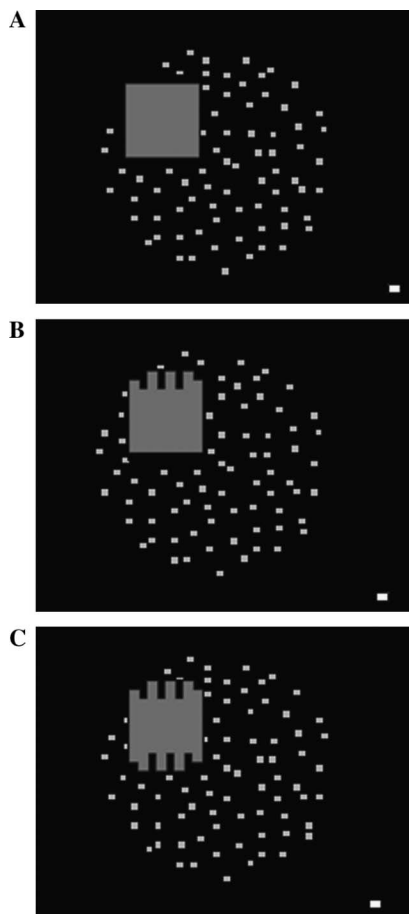


Fig. 5. Stimuli of Experiment 3: (A–C) show MIB displays with targets with increasingly long boundaries. Target size is held constant.

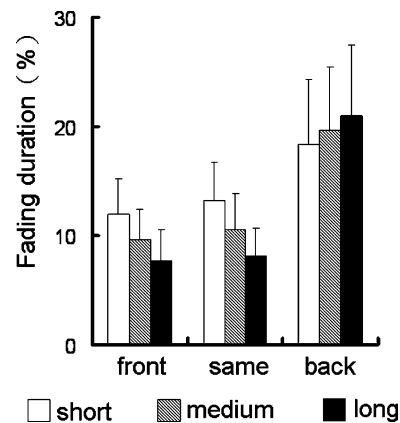


Fig. 6. Results of Experiment 3: the abscissa shows whether the target appeared in front of the distracters, at the same depth, or behind them. The white bars show the results for a target with a short boundary, the hatched bars the results for a target with a medium long boundary, and the black bars the results for a target with a long boundary. The ordinate shows the percentage of the total duration that the target was perceived to have disappeared, and the error bars represent 1 standard error.

5.37 , $p < .01$) and disparity (Wilk's lambda = .35, $F(2,22) = 20.69$, $p < .001$; univariate $F(2,46) = 33.12$, $p < .001$). In addition, their interaction was also significant (Wilk's lambda = .50, $F(4,20) = 4.95$, $p < .001$; univariate $F(4,92) = 6.11$, $p < .001$). Within participants, 48% of the variance was due to the experimental manipulations. Contrasts revealed that when the target had a positive or zero disparity, longer boundary lengths led to less MIB ($F(2,138) = 6.67$, $p < .01$, when the disparities were positive, and $F(2,138) = 8.53$, $p < .001$, when they were zero). When the target had a negative disparity, longer boundary lengths did not lead to less MIB ($F(2,138) = 2.42$, $p > .09$). These results replicate those of Experiment 2.

6. Experiment 4: Radial frequencies and depth in MIB

In this experiment, like in the previous one, only an MIB display was used. Boundary length was now manipulated by changing the shape of the target, while not only holding its size constant, but also its spatial frequency profile.

6.1. Method

6.1.1. Stimuli

Just like in Experiment 3, only an MIB display was used. The target's shape (Fig. 7) was now defined by the fourth derivative of a Gaussian (D4; Wilkinson, Wilson, & Habak, 1998). A cross section of the contour of this shape shows a wavy luminance profile in which the amplitudes of different spatial frequencies are limited by a smooth envelop that falls off with the distance away from the center of the contour. While keeping the spatial frequency profile of the D4 target constant in this way, its radial frequency—that determines its shape—was manipulated, and could be either 1, 3, or 5 cycles per D4 target. The radial frequencies had an amplitude of .2. The target had a mean luminance of 50 cd/

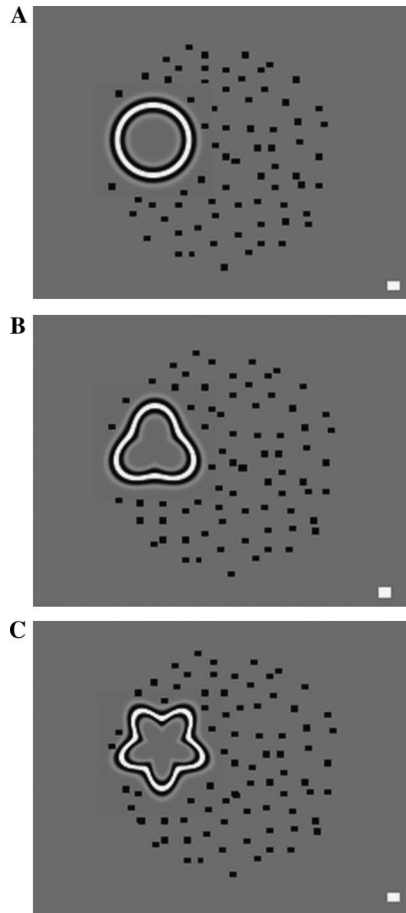


Fig. 7. Stimuli of Experiment 4: (A–C) show MIB displays with targets with the radial frequencies of 1, 3, and 5 cycles per target, respectively, causing the boundary in (A) to be the shortest, in (B) the second longest, and in (C) the longest, while holding target size constant.

m^2 , a mean radius of $.41^\circ$, and a σ of 3. The latter keeps the spatial frequency profile of the target constant, with a peak frequency of 7.25 cycles per degree. The targets used in this experiment were somewhat bigger than in Experiments 2 and 3, and they are therefore expected to lead to less MIB. However, this somewhat larger target size was necessary to allow the D4 pattern to become clearly visible, and to ensure that spatial frequency control was really achieved. In all other respects, this experiment was similar to Experiment 2. In total, it contained 9 conditions (3 different boundary lengths \times 3 different target disparities), and each condition contained six trials.

6.2. Results and discussion

Fig. 8 shows the results. A multivariate analysis of variance revealed significant effects of boundary length (Wilk's lambda = .45, $F(2,22) = 13.64$, $p < .001$; univariate $F(2,46) = 20.15$, $p < .001$) and disparity (Wilk's lambda = .06, $F(2,22) = 168.65$, $p < .001$; univariate $F(2,46) = 180.83$, $p < .001$). The interaction was marginally significant (Wilk's lambda = .65, $F(4,20) = 2.64$, $p = .06$; univariate $F(4,92) = 2.34$, $p = .06$). Within participants, 86% of the variance was

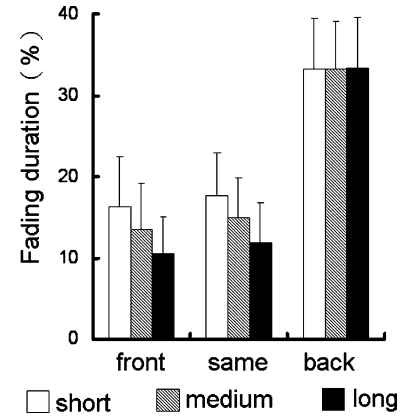


Fig. 8. Results of Experiment 4: the abscissa shows whether the target appeared in front of the distracters, at the same depth, or behind them. The white bars show the results for a target with a short boundary (small radial frequency), the hatched bars the results for a target with a medium long boundary (medium radial frequency), and the black bars the results for a target with a long boundary (large radial frequency). The ordinate shows the percentage of the total duration that the target was perceived to have disappeared, and the error bars represent 1 standard error.

due to the experimental manipulations. Contrasts revealed that when the target had a positive or zero disparity, longer boundary lengths led to less MIB ($F(2,138) = 11.28$, $p < .001$, when the disparities were positive, and $F(2,138) = 12.09$, $p < .001$, when they were zero). When the target had a negative disparity, longer boundary lengths did not lead to less MIB ($F(2,138) = 1.05$, $p > .5$). These results once again replicate those of Experiment 2.

7. General discussion

Experiment 1 demonstrated a boundary adaptation effect in MIB. In this experiment, pre-adaptation of random-dot patterns and of frames that did not fit the boundary of the target had little effect on MIB, but pre-adaptation of a frame that exactly fitted the boundary increased the MIB considerable, just as predicted. Experiment 2 demonstrated both a depth and a boundary adaptation effect, in both PFI and MIB. In this experiment, PFI and MIB both increased when the target appeared behind the distracter pattern (the *depth effect*), and both increased when the target was reduced in size (the *boundary adaptation effect*). Experiment 3 replicated the boundary adaptation effect on MIB and its interaction with the depth effect. In this experiment, a target with an irregular, long boundary caused less MIB than a target with a regular, short boundary, despite controlling for target size. Experiment 4, finally, replicated the boundary adaptation effect on MIB once again, and also its interaction with the depth effect. In this experiment, targets with low radial frequencies, and therefore short boundaries, caused more MIB than targets with high radial frequencies, despite controlling for both target size and spatial frequency. Thus, we have shown that boundary adaptation affects both PFI and MIB, and that the depth of the target relative to the distracter patterns

also affects both PFI and MIB. These results corroborate the conjecture by Hsu et al. (2004) that PFI and MIB share a common mechanism (or perhaps several common mechanisms), and are actually two manifestations of the same phenomenon.

Spillmann and De Weerd (2003) integrated early theories of PFI into one according to which the boundaries that segregate figure from ground are adapted, followed by the interpolation of the ground across these boundaries, which subsequently renders the figure invisible. However, Graf et al. (2002) have shown that MIB is affected by the relative order of depth of the target and the distracter pattern, and we have shown that the same is true for PFI too (Experiment 2). These results are difficult to relate to boundary adaptation, and hence, challenge those accounts that are based solely on it.

In the model of Grossberg and colleagues, near boundaries inhibit those that are farther away in depth (e.g., Kelly & Grossberg, 2000; Grossberg & Yazdanbakhsh, 2005). This could potentially explain why targets in back disappear out of view more easily than targets in front, both in PFI and in MIB, if it is assumed that weak boundaries require less adaptation than strong ones to fade away. In their model, however, near boundaries only inhibit those farther away in those locations where they spatially overlap, and in our MIB displays there were rarely any overlapping or even abutting boundaries. Hence, their model could only explain our data, if the inhibition were fairly broadly tuned, and also included nearby boundaries rather than only overlapping ones.

Bonneh et al. (2001) and Sagi and Gorea (2003) had a very different approach, and suggested that shifts of attention could be the cause of MIB. If they are right, and if it is assumed that a target in front receives more attention than a target in back, then a lack of attention for the target in back could indeed explain the MIB results of Graf et al. (2002), as well as the depth effects that we found here in PFI.

In PFI and MIB some stimuli (i.e., targets) disappear from view, and in this respect, these phenomena are similar to monocular and binocular rivalry. Mitchell, Stoner, and Reynolds (2004) have shown that lack of attention is at least in part responsible for disappearance during binocular rivalry, and therefore lends some support to this conjecture. Moreover, that stimuli do indeed attract more attention when they appear in front rather than in back is also suggested by the results of Wong and Weisstein (1982) who showed that line detection is easier when a line appears on a figure than when it appears on a ground. Mazza, Turatto, and Umilta (2005) obtained similar results, using a change blindness paradigm.

7.1. Summarizing this discussion

The effect of boundary adaptation is well-documented. We replicated it in various ways in this article too, and showed that it affects both PFI and MIB. However, we did not find evidence for boundary adaptation when targets were presented behind distracter patterns, despite that we

consistently found it when targets were presented in front of them, or in the same depth plane. Perhaps Bonneh et al. (2001) and Sagi and Gorea (2003) were right that shifts of attention could be a cause of MIB too, and if so, then they are in all likelihood a cause of PFI as well. Alternatively, Graf et al. (2002) could also be right that the completion of a surface in front of a target could be a cause of MIB (and therefore most probably also of PFI), but in this case it has to be explained why—contrary to expectation—these surfaces would always be opaque and occluding the target, rather than transparent and leaving it visible. In any event, on the one hand, our results suggest that the mechanism underlying PFI and MIB involves boundary adaptation. On the other hand, the depth effect also shows that boundary adaptation can be no more than a sufficient cause of PFI and MIB, and not a necessary one.

References

- Anstis, S. (1989). Kinetic edges become displaced, segregated and invisible. In D. Man-Kit Lam & C. D. Gilbert (Eds.), *Neural mechanisms of visual perception* (pp. 247–260). Houston, TX: Gulf Publishing.
- Anstis, S. (1996). Adaptation to peripheral flicker. *Vision Research*, *36*, 3479–3485.
- Blakemore, C., & Julesz, B. (1971). Stereoscopic depth aftereffect produced without monocular cues. *Science*, *171*, 286–288.
- Bonneh, Y. S., Cooperman, A., & Sagi, D. (2001). Motion-induced blindness in normal observers. *Nature*, *411*, 798–801.
- Davey, M. P., Maddess, T., & Srinivasan, M. V. (1998). The spatiotemporal properties of the Craik-O'Brien-Cornsweet effect are consistent with “filling-in”. *Vision Research*, *38*, 2037–2046.
- De Weerd, P., Desimone, R., & Ungerleider, L. G. (1998). Perceptual filling-in: A parametric study. *Vision Research*, *38*, 2721–2734.
- De Weerd, P., Gattass, R., Desimone, R., & Ungerleider, L. G. (1995). Responses of cells in monkey visual cortex during perceptual filling-in of an artificial scotoma. *Nature*, *377*, 731–734.
- De Weerd, P., & Pessoa, L. (2003). Introduction: Filling-in: More than meets the eye. In L. Pessoa & P. De Weerd (Eds.), *Filling-in: From perceptual completion to cortical reorganization* (pp. 1–10). New York: Oxford University Press.
- Francis, G., Grossberg, S., & Mingolla, E. (1994). Cortical dynamics of feature binding and reset: Control of visual persistence. *Vision Research*, *34*, 1089–1104.
- Graf, E. W., Adams, W. J., & Lages, M. (2002). Modulating motion-induced blindness with depth ordering and surface completion. *Vision Research*, *42*, 2731–2735.
- Gerrits, H. J. M., De Haan, B., & Vendrik, A. J. H. (1966). Experiments with retinal stabilized images. Relations between observations and neural data. *Vision Research*, *6*, 427–440.
- Grossberg, S. (1994). 3-D vision and figure-ground separation by visual cortex. *Perception & Psychophysics*, *55*, 48–121.
- Grossberg, S., & Yazdanbakhsh, A. (2005). Laminar cortical dynamics of 3D surface perception: Stratification, transparency, and neon color spreading. *Vision Research*, *45*, 1725–1743.
- Hsu, L.-C., Yeh, S.-L., & Kramer, P. (2004). Linking motion-induced blindness to perceptual filling-in. *Vision Research*, *44*, 2857–2866.
- Kelly, F., & Grossberg, S. (2000). Neural dynamics of 3D surface perception: Figure-ground separation and lightness perception. *Perception & Psychophysics*, *62*, 1596–1618.
- Mazza, V., Turatto, M., & Umilta, C. (2005). Foreground-background segmentation and attention: A change blindness study. *Psychological Research*, *69*, 201–210.
- Mitchell, J. F., Stoner, G. R., & Reynolds, J. H. (2004). Object-based attention determines dominance in binocular rivalry. *Nature*, *429*, 410–413.

- Neumann, H., & Mingolla, E. (2001). In T. H. Shipley & P. J. Kellman (Eds.), *From fragments to objects—Segmentation and grouping in vision* (pp. 353–400). Amsterdam: Elsevier Science Publishers.
- Ramachandran, V. S. (2003). Foreword. In L. Pessoa & P. De Weerd (Eds.), *Filling-in: From Perceptual Completion to Cortical Reorganization*. (pp. xi–xxii). New York: Oxford University Press.
- Ramachandran, V. S., Gregory, R. L., & Aiken, W. (1993). Perceptual fading of visual texture borders. *Vision Research*, *33*, 717–721.
- Ramachandran, V. S., & Gregory, R. L. (1991). Perceptual filling of artificially induced scotomas in human vision. *Nature*, *350*, 699–702.
- Sagi, D., & Gorea, A. (2003). Natural extinction. Paper Presented at 26th European Conference on Visual Perception, Paris, France.
- Sereno, M. I., Dale, A. M., Reppas, J. B., Kwong, K. K., Belliveau, J. W., Brady, T. J., et al. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*, *268*, 889–893.
- Spillmann, L., & De Weerd, P. (2003). Mechanisms of surface completion: Perceptual filling-in of texture. In L. Pessoa & P. De Weerd (Eds.), *Filling-in: From perceptual completion to cortical reorganization* (pp. 81–105). New York: Oxford University Press.
- Spillmann, L., & Kurtenbach, A. (1992). Dynamic noise backgrounds facilitate target fading. *Vision Research*, *32*, 1941–1946.
- Tabachnick, B. G., & Fidell, L. S. (1989). *Using multivariate statistics*. New York: Harper Collins Publishers, Inc.
- Wong, E., & Weisstein, N. (1982). A new perceptual context superiority effect: Line segments are more visible against a figure than against a ground. *Science*, *218*, 587–589.
- Wilkinson, F., Wilson, H. R., & Habak, C. (1998). Detection and recognition of radial frequency patterns. *Vision Research*, *38*, 3555–3568.