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Perceptual filling-in: a parametric study

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Abstract

We studied perceptual filling-in during maintained peripheral viewing of a uniform gray or red figure presented on a large textured background. Changes in the figure's size, shape, and eccentricity caused variations in the time required for filling-in that could be predicted from the size of its cortical projection within early visual areas. The data suggest that the time which elapsed before the figure was filled-in by its background reflects the time required for figure-ground segregation to fail, rather than a slow spread of the background across the figure. Our findings reveal interactions between surface segregation and filling-in which may be at the basis of normal surface perception. Published by Elsevier Science Ltd. All rights reserved.

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1. Introduction

The fact that we do not perceive an 'empty' region in our visual field corresponding to the blind spot indicates that the visual system perceptually fills-in the blind spot with the information surrounding it. Similar types of perceptual filling-in have been reported for pathological scotomas [1,2]. Furthermore, it has been reported that stabilizing the image of a spot on the retina leads to perceptual filling-in of the spot with the surrounding background. Perceptual filling-in of stabilized images has been demonstrated for color and brightness [3–6], and recently, similar findings have been reported for texture [7–9].

It has been suggested that perceptual filling-in of scotomas and stabilized images is a manifestation of a filling-in process that also takes place during normal surface perception [10,11]. A direct demonstration of filling-in during normal surface perception was provided by Paradiso and Nakayama [12]. In their experiment, subjects were presented with a bright disk flashed on a dark background, followed almost immediately by a masking stimulus consisting of a grid of white contours. Subjects reported seeing a bright annulus with a dark center, as if the contours of the mask had interrupted the spread of brightness inward from the disk's outer edge. By varying the types of masks used and the time interval between the presentation of disk and mask, Paradiso and Nakayama [12] found that the perception of surface brightness depends upon an active process during which brightness is filled-in from a surface's outer edge towards its middle, over the course of a few tens of milliseconds. Related examples of the role of filling-in, or interpolation, in surface perception are the perception of depth in stereograms [13] and the perception of depth in the orthographic projection of texture on a transparent, rotating cylinder [14]. Because similar neural mechanisms may be involved in all of these phenomena, the study of perceptual filling-in could provide insight into mechanisms of normal surface perception.

There has been little parametric work to determine the precise conditions under which perceptual filling-in occurs. We investigated the properties of filling-in during maintained peripheral viewing of a dynamic texture made of jittering horizontal line segments, with an equiluminous region in its middle devoid of texture. We explored the effects of several factors on perceptual filling-in, including the effects of the middle region's size, stability, eccentricity, shape and color, and the effects of the relative sizes of the middle region and surrounding texture.

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2. Methods

In a typical experiment, subjects were instructed to fixate a red fixation dot presented in the middle of a computer screen, and to maintain fixation while a homogeneous gray or red region (square, rectangle, or annulus segment) was presented surrounded by a dynamic texture. Subjects initiated each trial by pressing the spacebar on a computer keyboard, and pressed a button to indicate filling-in of one region by the other. The minimum time between consecutive trials was about 4 s. Before each experiment, subjects performed approximately ten trials in a representative set of experimental conditions, and they were encouraged to develop a consistent criterion with which to judge perceptual filling-in, based on perceived similarity between the filled-in and surrounding regions in the stimulus. Unless otherwise indicated, the texture was $16 \times 16°$ in size, and was centered in the lower left quadrant of the visual field. The homogeneous region in the center was equiluminous with the average luminance of the surrounding dynamic texture, and with the gray background upon which the texture was presented (23 cd/m^2). The dynamic texture was a 'movie' made of 5 frames, each of which consisted of horizontal, white line segments ($0.7 \times 0.1°$) on a dark background, spaced 0.4° apart on average. Since the position of the line elements was randomized in each frame of the movie, playing the movie (at 20 Hz) created a stimulus with continuously jittering line segments. Stimuli were generated with a Number Nine Pepper SGT graphics card, and presented on a color monitor with 480×640 pixel resolution and a 60 Hz refresh rate. Subjects viewed stimuli on the monitor from a distance of 35 cm, unless otherwise indicated. Experimental conditions were randomly interleaved.

3. Results

3.1. Experiment 1: effect of square size

To investigate the spatial extent over which filling-in mechanisms operate, we manipulated the size of a gray square surrounded by texture, and asked subjects to report filling-in of the square by the texture with a button press. This experiment also allowed us to assess the effect of changes in the square's size on the time course of filling-in. The square's size is given by the length of its side, which varied from 0.6 to 5.6°. All squares were presented at an eccentricity of 8° from the fixation spot. On any trial, we presented the stimulus for a maximum of 20 s. Upon a response, the stimulus was turned off, after which subjects initiated a new trial. Four subjects (MA, RH, BJ, and AL) performed ≈ 20 trials in each experimental condition, or about 120 trials per session. Fig. 1(A) shows a typical example of a stimulus used in this experiment.

Fig. 1(B) shows for four subjects that the median time required to perceive filling-in increased from about 3 s at the smallest square sizes to about 10 s at the largest size tested (5.6°). This increase is also evident in Fig. 1(C), which shows separately for each subject the cumulative proportion of trials with filling-in as a function of time for different square sizes. In each subject, the curves representing cumulative proportions of trials with filling-in show a rightward shift with increasing square size, indicating that filling-in of the square took progressively more time as its size was increased. Filling-in was not always observed with a square size of 5.6°, suggesting that a gap of 5.6° approaches the spatial limit for filling-in at an eccentricity of 8°. Because filling-in did not always take place for the largest

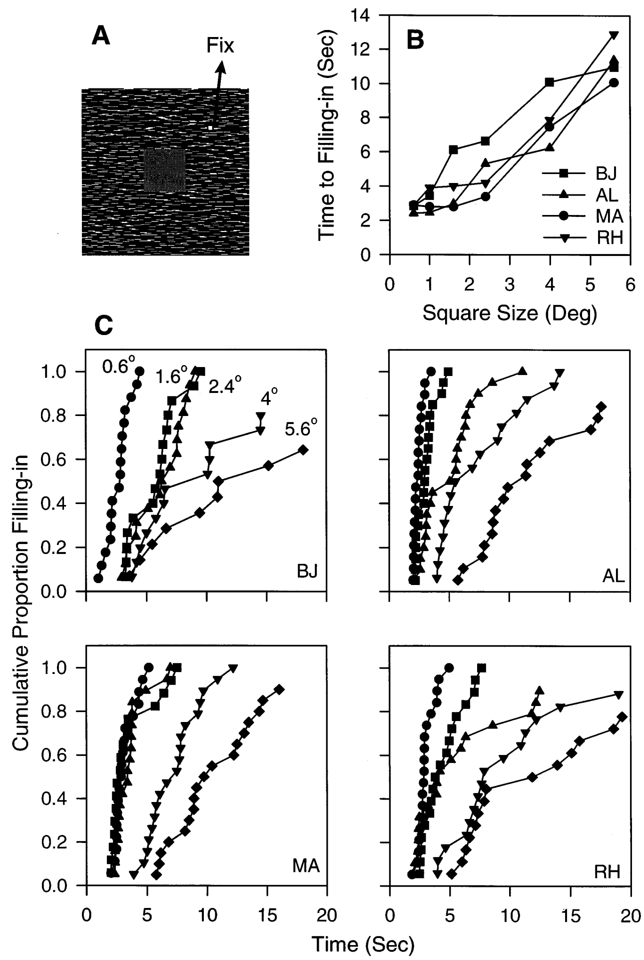

Fig. 1. Perceptual filling-in of gray squares of different sizes by a dynamic texture background. The squares were presented at 8° of eccentricity. (A) Typical stimulus used in experiment 1. The small white square indicates the position of the fixation point (Fix). (B) Median time to filling-in plotted as a function of square size for four subjects. (C) Cumulative proportion of filling-in responses as a function of time for square sizes ranging from 0.6 to 5.6°, as labeled in upper left panel, shown for subjects BJ, AL, MA, and RH. Square size refers to the length of the square's side.

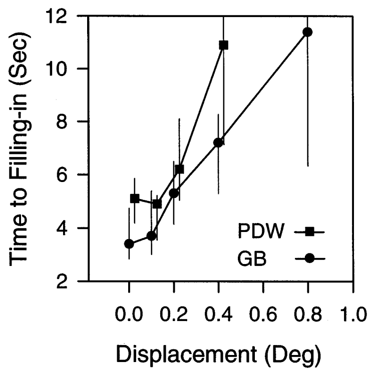

Fig. 2. Median time required to perceive filling-in as a function of the displacement of the square, shown in two subjects (GB and PDW). Square size was 2.4°, and the eccentricity was 8°. Displacements along the diagonals of the square occurred each second throughout each 12 s trial. Error bars indicate the 25th and 75th percentiles. The data from PDW are plotted with a small offset to the right, to allow for the error bars in both subjects.

sizes, performance is summarized using medians in Fig. 1(B), and in subsequent figures. The use of medians allowed us to include trials without filling-in into the estimated filling-in time, since trials without filling-in can be considered as trials with a filling-in time larger than the stimulus exposure.

3.2. Experiment 2: effect of the stability of the square on perceptual filling-in

Several investigators have argued that filling-in is a consequence of the adaptation of the boundary representations that separate neighboring parts of the image [7,10,15,16]. If filling-in required the adaptation of the square's boundaries during maintained fixation, then shifting its boundaries should prevent filling-in. To test this prediction, we slightly changed the position of the square after each second during each 12-s trial. During a single 1-s epoch of the trial, the square could be in any of five possible positions: the default position at an eccentricity of 8° and four additional positions resulting from up or down displacements along left and right oblique axes. The square's side was 2.4°, and the magnitudes of the displacements were 0, 0.1, 0.2, 0,4, 0.8 and 1.6°, tested in six separate conditions. Two subjects (GB and PDW) performed about 20 trials in each condition.

The median time required to perceive filling-in increased rapidly with increasing displacements of the square (Fig. 2). A Mann–Whitney *U*-test on data pooled over both subjects revealed that displacements of just 0.2° resulted in a significant delay of filling-in compared to filling-in without displacements [$U = 389$, $n = 40$, $P < 0.001$]. Displacements of 0.4° doubled the time required to perceive filling-in (Fig. 2), and displacements > 0.4 and 0.8° in subjects PDW and GB, respectively, prevented filling-in during virtually all trials. In separate experiments (unpublished data), we found that moving the entire background texture at the same rate (once each second) and over the same distances, while holding the square stationary, did not affect the time required to perceive filling-in of the square. Thus, the effects of moving the square are specifically due to displacements of the square's borders, and not to the displacements of other contours in the surrounding texture.

The data suggest that accurate fixation (probably within a few tenths of a degree) is necessary to obtain fast filling-in, and that differences between subjects in the time required to perceive filling-in may reflect differences in the accuracy of fixation. For example, the data in Fig. 2 show that subject PDW was slower to fill-in the square than subject GB, even without displacements of the square. Further, filling-in was prevented with smaller square displacements in subject PDW than in subject GB, possibly because retinal displacements caused by fixation errors in subject PDW were larger to begin with.

Displacements of the square's boundaries on the order of a few tenths of a degree delayed filling-in, but the filling-in process could span squares up to 5.6° across under conditions of accurate fixation. Thus, the filling-in process can bridge gaps that are much larger than the boundary displacements that disrupt it. This finding supports the notion that perceptual filling-in relies on the adaptation of boundary representations, which allows another, separate mechanism to fill-in the square.

3.3. Experiment 3: the effect of the size of the texture on perceptual filling-in

We next manipulated the width of the textured region surrounding the square, referred to as the width of the 'texture frame', using a range of different square sizes. We performed this experiment to answer three questions. First, we wished to determine the width of the texture frame required for filling-in in order to provide further information about the spatial extent of the filling-in mechanism. Second, we wished to investigate the possibility that perceptual filling-in results from a competition between the representations of different regions in the image, during which the 'strongest' representation wins over the 'weaker' one. For example, stimuli in which the texture frame is narrow relative to the size of the square might lead to filling-in of the texture field by the gray in the square instead of the opposite, more commonly reported result (Section 3.1). Third, we wished to determine whether the effect of square size on the time required to perceive filling-in was confounded with the effect of decreases in the width of the texture frame around the square. In previous experiments, the total size of the stimulus was confined to a 16 × 16° square area, such that increases in square size led to a reduced width of the surrounding texture frame. In the present experiment, we independently manipulated square size and frame width. Four different squares were used (1, 2, 4 or 6°), presented at an eccentricity of 8°. Each square was presented within eight texture frame widths ranging from 0.1 to 8°. Four subjects were instructed to press a key to indicate when the square filled-in, and another key to indicate the disappearance of the texture field caused by filling-in of the texture field by the gray inside the square. After any response, the trial was aborted. Stimuli were presented for a maximum of 20 s. Four subjects (PDW, JF, JN, and MR) performed an average of 12 trials in each experimental condition.

After pooling the data over the four subjects, we found that the percentage of trials with filling-in ranged from zero to 100% depending on the width of the texture frame, and that the median time required to perceive filling-in decreased as the texture frame was increased (Fig. 3A). In addition, the width of the texture frame required for filling-in depended upon the size of the square. For example, a narrow frame of just 0.4° was sufficient to obtain very frequent and fast filling-in of a square of 1° (arrows in Fig. 3A), while the same frame width was insufficient to produce reliable filling-in for the three larger squares used. To quantify the relationship between the width of the texture frame required for filling-in and square size, we used linear interpolation between neighboring data points to calculate the frame width required to perceive filling-in in 50% of the trials for each square size (Fig. 3B). We found that the frame width required to obtain filling-in on 50% of the trials increased from 0.3° at a square size of 1°, to 3.4° at a square size of 6.4°. For square sizes up to 4°, the relationship between square size and frame width was nearly linear (Fig. 3B). At these smaller square sizes, surprisingly little surrounding texture was required to obtain filling-in in a significant number of trials. For example, at a square size of 4°, filling-in was observed in 62% of the trials with a texture frame width of just 1° (Fig. 3A). Beyond square sizes of 4°, the minimum frame width for filling-in increased significantly (Fig. 3B).

On trials in which the texture frame was narrow relative to the size of the square, the square often did not fill-in. Rather, in many trials (but not all), the texture frame disappeared and was perceptually replaced with the gray of the square and the gray background upon which the texture frame was presented. This is illustrated in Fig. 4 for each of the four square sizes used. The data suggest that filling-in involves a competition between the representations of the texture frame and the gray regions within and beyond it, with the winning representation invading the other one. Increasing the size of one representation relative to the other biases the outcome of this competition. Note that the term 'filling-in' has the connotation that the featural spread beyond physically present boundaries during perceptual filling-in is uni-directional. We will continue to use the term 'filling-in', with the understanding that it refers to a bi-directional process of featural spread.

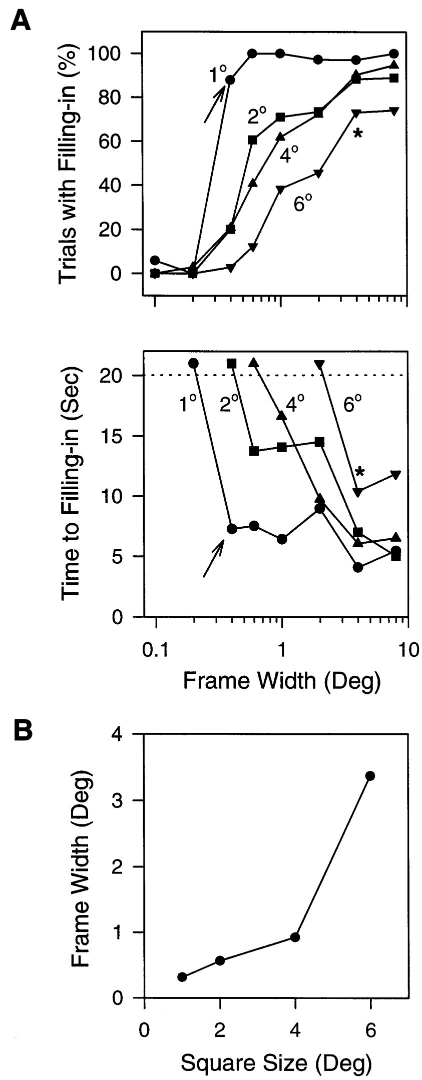

Fig. 3. Study of the effects of the width of the surrounding texture (frame width) on perceptual filling-in of squares ranging in size from 1 to 6°. (A) Percent trials with filling-in plotted as a function of frame width for square sizes of 1, 2, 4 and 6°, as labeled in the figure (top), and median time required for filling-in as a function of frame width for different square sizes, as indicated by labels in the figure panel (below). Symbols above the dotted line indicate experimental conditions in which subjects perceived filling-in on less than half of the trials. (B) Frame width for which 50% of the trials resulted in perceptual filling-in, plotted as a function of square size. Results were pooled over subjects (JF, JN, MR, PDW). The arrows in upper and lower panels of A indicate the smallest frame width at which frequent and fast filling-in occurred (0.4°), with a hole size of 1°. The asterisks in upper and lower panels of A indicate the frame width at which the rate and time course of perceptual filling-in assymptotes (4°), with a hole size of 6°. For explanations of arrows and asterisks in A and B, see Section 3.3.

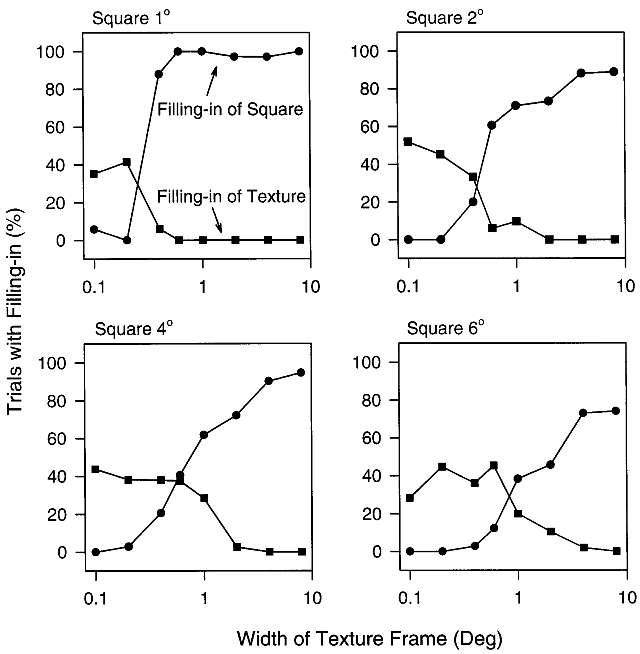

Fig. 4. Percent trials with filling-in as a function of frame width for square sizes of 1, 2, 4 and 6°. Solid dots indicate filling-in of the gray square by the surrounding texture, while solid squares indicate filling-in of the texture by the gray of the square, and of the background upon which the texture is presented. Results were pooled over subjects (PDW, JF, JN, MR).

The results from the present experiment also demonstrate that the effects of square size on the time required to fill-in the square in experiment 1 were not confounded with effects of texture frame width. Even for the largest square (5.6° square in a 16 × 16° texture field), the width of the texture frame around the square exceeded 4°, which is larger than the frame width at which the efficiency of filling-in asymptotes at a similar square size of 6° (see asterisks in Fig. 3A).

3.4. Experiment 4: perceptual filling-in of two squares in a texture

The previous experiment showed that a relatively narrow frame of texture is sufficient to cause filling-in of the region enclosed by it. This finding suggests that retinotopically localized mechanisms might play an important role in filling-in. If filling-in depended on such localized mechanisms, then two neighboring squares in a large texture should not necessarily fill-in at the same time. Alternatively, it is possible that filling-in is mediated by a mechanism located in an area such as inferior temporal cortex, where cells have large receptive fields encompassing the texture and both squares [17,18]. Such cells might 'decide' for both squares simultaneously when both are perceived as filled-in. To test these alternative possibilities, we measured the time to fill-in two squares presented simultaneously in a texture background occupying the entire screen. Each square measured 3.2 × 3.2°, and both were placed at 8° from the fixation point. The arrangement of the squares is shown schematically in the inset in Fig. 5. Two subjects (PDW and MR) were instructed to press one button in their left hand to indicate filling-in of the left-most square, and to press another button with their right hand to indicate filling-in of the right-most square. Each subject performed 30 trials. Stimuli were presented for up to 20 s, or until a filling-in response was recorded for both squares.

Fig. 5 shows the frequency distribution of the absolute time differences with which the two neighboring squares filled-in, after pooling the data from both subjects. When asked to press the two buttons simultaneously, in the absence of any stimuli, the time difference in the button presses was systematically < 100 ms in both subjects. Therefore, one could argue that all filling-in trials in which the button presses were more than 100 ms apart (52%) indicated filling-in of the two squares at different times. In 30% of the trials the time difference was at least 500 ms, and in 20% of the trials it was more than 1 s. These trial-by-trial differences could not be explained by an overall bias to fill-in one square faster than the other. The median response times with left and right buttons occurred after 4054 and 3988 ms, respectively, and the difference was not statistically significant (sign test, $n = 60$, $P = 0.19$). The results thus support the view that mechanisms operating with a limited spatial range, and acting at least partially independently at different retinal locations, contribute to perceptual filling-in.

3.5. Experiment 5: relationship between effects of square size and eccentricity

If perceptual filling-in were mediated by mechanisms that act independently at different locations in the visual field, then those mechanisms might be located in visual cortical areas that show retinotopy. Retinotopi-

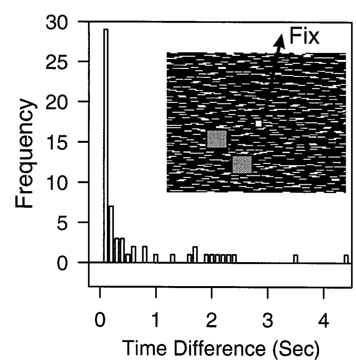

Fig. 5. Distribution of differences in the time after which two simultaneously presented squares fill-in. The inset offers a schematic overview of the stimulus. The gray squares (3.2°) were presented at 8° from the fixation point (Fix). Trials were pooled over two subjects (PDW and MR).

cally organized areas show a decrease of cortical magnification with increases in eccentricity [19]. As a consequence, the effect of increases in square size on perceptual filling-in should be similar to the effect of decreases in the square's eccentricity, because both manipulations result in an increased cortical representation of the square. To test these ideas, perceptual filling-in was measured in three subjects (PDW, DP, and CRH) for squares ranging in size from 0.1 to 7°, presented at eccentricities of 2, 4, 6, 8, 12 and 20°. Viewing distance was 57 cm, instead of the 35 cm in previous experiments, but the size and spacing of the texture elements were multiplied by a factor of 1.63 to keep the textures similar to the ones used in previous experiments. The entire display area of the monitor was filled with texture, and to present the stimuli in the left lower quadrant of the visual field we positioned the fixation spot in the upper right hand corner of the computer screen. On each trial, the stimulus was presented for up to 20 s. The subjects were instructed to press a button whenever the square was filled-in completely, upon which the trial was aborted. The three subjects (PDW, DP, and CRH) performed approximately 10 trials at each size and eccentricity.

In a preliminary experiment, subjects found it difficult to report filling-in of squares at eccentricities beyond 12°, because in many instances the presence of the square was unclear from the beginning of the trial. We found, however, that using squares that were red in color, equiluminant with the surrounding texture, enabled subjects to perceive the square clearly from the beginning of the trial, and to report subsequent filling-in. The experiments reported on below were carried out using a red square.

Fig. 6A shows the percentage of trials with filling-in as a function of the size of the square at six different eccentricities. Each data point was obtained after pooling over the three subjects. At an eccentricity of 2°, filling-in was observed in all trials for small squares up to 0.6° in size. Increasing their size further to 1° caused a sudden drop in the incidence of filling-in to 55% of the trials. By contrast, at an eccentricity of 20°, squares of up to 7° were filled-in 100% of the time. Intermediate results were observed at intermediate eccentricities. Similarly, the median time required to perceive filling-in (calculated on pooled data; Fig. 6B) increased rapidly with increasing square size at an eccentricity of 2°, whereas the increase in time to filling-in as a function of square size became less pronounced at higher eccentricities.

Fig. 6 demonstrates that a small increase in the size of the square caused long delays in perceptual filling-in at small eccentricities, while the same increase in size had smaller effects at larger eccentricities. This finding parallels the fact that a small increase in square size at small eccentricities corresponds to a large increase in the size of its cortical projection, while the same increase in square size at a larger eccentricity corresponds to a smaller increase in cortical projection size. This is due to the decrease in cortical magnification with increasing eccentricity in retinotopically organized visual cortical areas [19]. To further test the idea that the time required to perceive filling-in is a function of the size of the square's cortical projection, rather than eccentricity or square size per se, we calculated the area of the cortical projection of each square at each eccentricity, based on estimates of human cortical magnification obtained with functional magnetic resonance imaging [20]. We then replotted the time required to fill-in the square as a function of the square root of cortical projection area. We used the square root of projection area instead of area, because a linear regression fit the data slightly better, although the difference between the

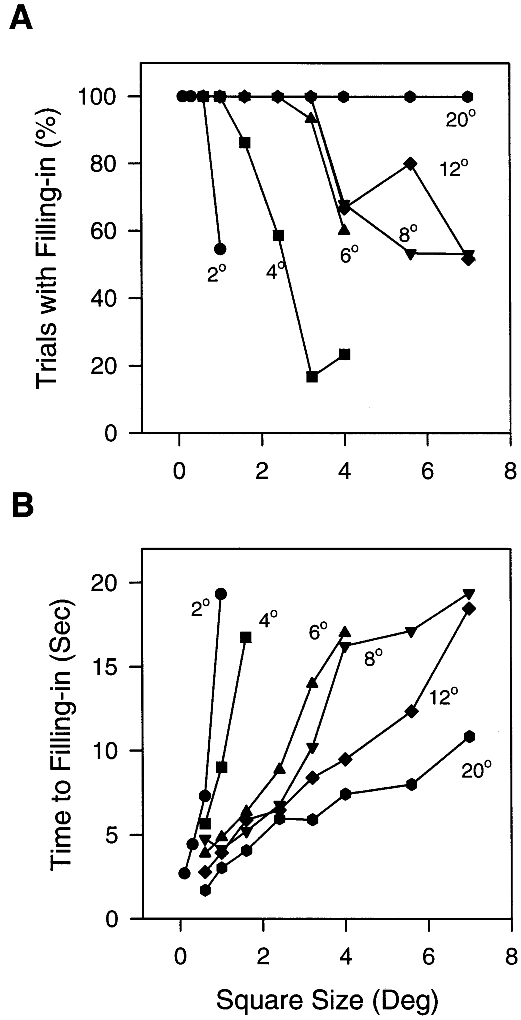

Fig. 6. Perceptual filling-in as a function of square size at eccentricities ranging between 2 and 20°. (A) Percent trials with filling-in plotted as a function of square size at six eccentricities. Labels next to the curves indicate eccentricities. (B) Median time to filling-in as a function of square size at six different eccentricities. Results are pooled over subjects (MA, RH, JN, PDW).

regressions for area versus square root of area was not statistically significant.

Fig. 7A shows the median time required to perceive filling-in plotted as a function of square size in degrees of visual angle, ignoring the fact that the data were obtained at different eccentricities (see Fig. 6B). A linear regression yielded a statistically significant, but relatively low coefficient of determination ($r^2 = 0.43$, $t = 5.42$, $n = 40$, $P < 0.01$). Each data point represents data pooled over subjects. Fig. 7(B) shows the same set of data, re-plotted as a function of the square root of cortical projection area, using cortical magnification factors of human cortical areas V1 and V3 (see Appendix). We obtained a strong linear relationship between time required for filling-in and the square-root of cortical projection area, as evidenced by the high coefficients of determination using the magnification factors in V1 ($r^2 = 0.88$) and V3 ($r^2 = 0.86$). The linear relationship between time required for filling-in and the square root of the square's cortical projection area (Fig. 7B) was significantly better than the relationship between time required for filling-in and square size measured by visual angle on the retina (Fig. 7A). This was true when using cortical magnification data from both V1 ($Z = 4.03$, $n = 40$, $P < 0.01$) and from V3 ($Z = 3.68$, $n = 40$, $P < 0.01$). Using cortical magnification data from V2 led to similar results.

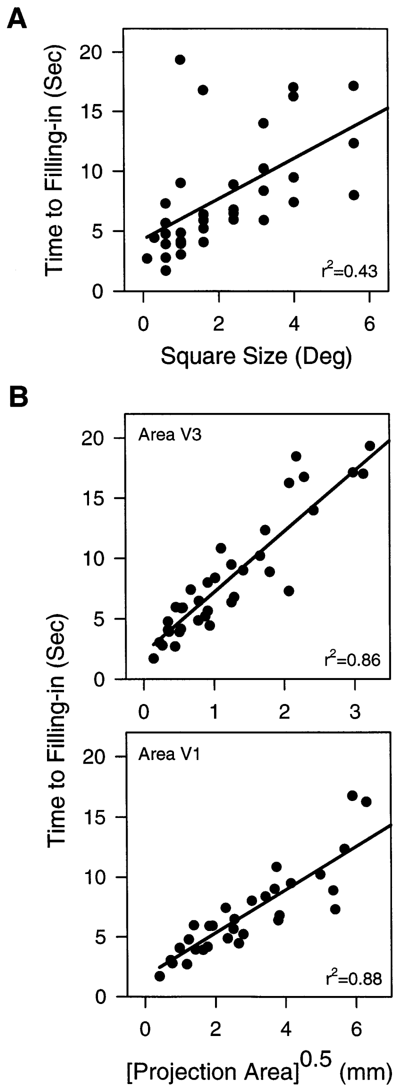

Fig. 7. Comparison of linear data fits before and after converting square size into cortical projection area in human area V1 and V3. (A) Median time required to perceive filling-in as a function of square size, ignoring the fact that the data points were obtained at different eccentricities. (B) Median time required to report filling-in as a function of square root of cortical projection area of the square, determined on the basis of cortical magnification factors in human V3 (upper panel) and human V1 (lower panel) reported by Sereno et al. [20]. The solid line in each figure panel indicates a linear regression through the data, and the coefficient of determination is shown in the lower right hand corner of each figure panel. Each data point represents pooled data from four subjects, taken from Fig. 6(B).

Since at any given eccentricity cortical magnification is larger in V1 than in extrastriate areas (note the different scales on the abscissa for areas V1 and V3 in Fig. 7B), one cannot conclude that the time to filling-in is related to the absolute size of the projection on the cortex. Our analysis shows, however, that the differences in time required to perceive filling-in of a red square resulting from manipulations of the square's eccentricity and size correlate with relative differences in the size of the square's cortical projection within a given visual area. The fact that this conclusion holds for different cortical areas reflects the similarity of the relative changes in cortical magnification as a function of eccentricity in early visual areas. Whenever we correlate differences in the time required to perceive filling-in with differences in cortical projection, we always refer to relative differences in cortical projection within a given visual area. Subsequent correlations between time to filling-in and cortical projection will be made exclusively on the basis of cortical magnification in area V3. This choice is arbitrary, except for the fact that a neurophysiological correlate of filling-in has been described in macaque area V3 (see Section 4).

It has been suggested that the time course of filling-in would be directly related to eccentricity, because eye movements at small eccentricities might be more disruptive for the adaptation of boundaries than at larger eccentricities, given the increasing size of receptive fields with increasing eccentricity (e.g. see ref. [8]). Our data do not support that idea, since squares presented at very different eccentricities filled-in after similar periods of peripheral fixation, provided their cortical projection areas were similar. Moreover, squares of very different retinal sizes showed similar filling-in times if their cortical projection areas were similar. Thus, we propose that the effects of the square's eccentricity and size on filling-in are caused by the same underlying factor, i.e. (relative) cortical projection area.

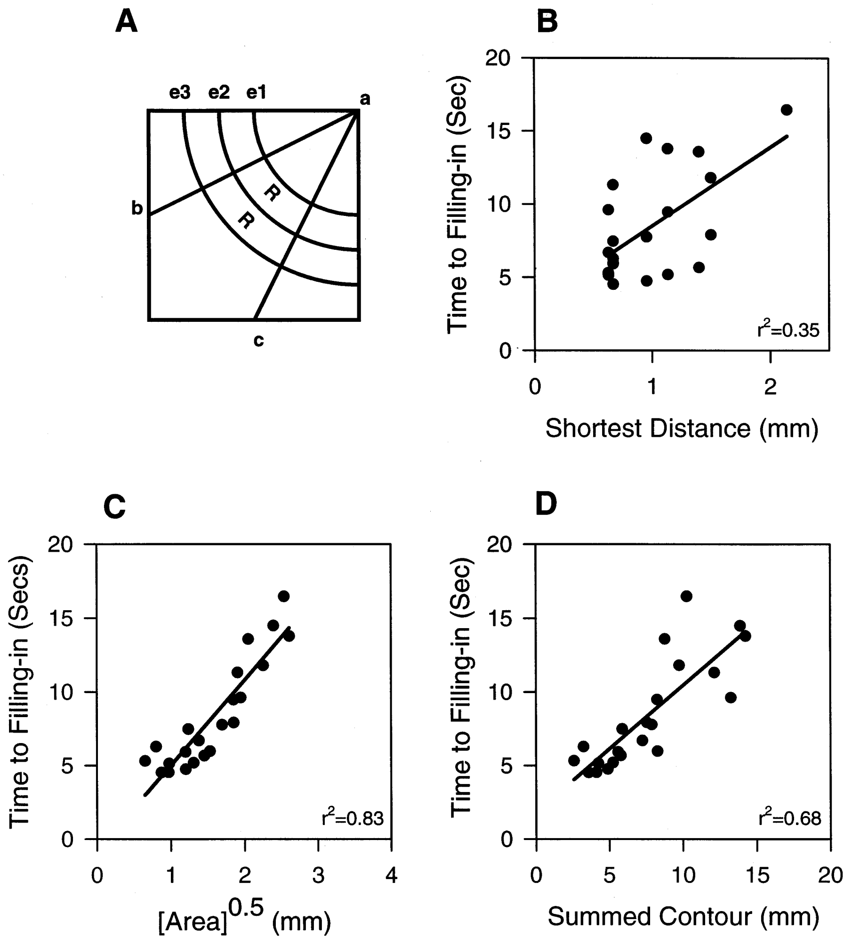

Fig. 8. Median time to fill-in segments of annuli of different sizes, presented at different eccentricities. (A) Scheme indicating lines of equal polar angle and iso-eccentricity lines defining the red annulus segments used in the experiment. Red regions in the image are labeled 'R'. See text for further explanations. (B) Median time to filling-in as a function of shortest distance across the cortical projection area in V3 of the annulus segments. (C) Median time to filling-in as a function of the square root of cortical projection area of the annulus segments. (D) Median time to filling-in as a function of the total length of the cortical representation of the annulus segments' boundaries. Other conventions as in Fig. 7. Data were pooled over two subjects (PDW and DP).

3.6. Experiment 6: dissociating effects of cortical projection area and cortical distance

If filling-in were due to the representation of the outer texture slowly invading the representation of the inner square, then the shortest distance across the square's cortical projection might predict the time required for filling-in. The strong correlation between the square root of projection area and the time required to perceive filling-in raised the possibility that the time required for filling-in is indeed correlated with the shortest distance across the square's projection. However, in the previous experiment, we were unable to distinguish between the effects of projection area and those of shortest distance across the area because these two factors were perfectly correlated with each other. In the present experiment, we replaced the squares with segments of annuli, which project as rectangles on the cortex. By manipulating the dimensions of the rectangular cortical projections we could dissociate the effects of cortical projection area from the effects of the shortest distance across the projection. The annulus segments were defined by the polar angle between line segments ab and ac (Fig. 8A), and by two iso-eccentricity lines. All annulus segments had iso-eccentricity line e2 in common, but in one set of annulus segments the second iso-eccentricity line (e1) was closer to the fixation point (a) while in another set of annulus segments the second iso-eccentricity line (e3) was farther away from the fixation point. Iso-eccentricity line e2 was 4° from fixation. Iso-eccentricity line e1 was at eccentricities of 2, 2.5, 3, or 3.5°. Iso-eccentricity line e3 was at eccentricities of 4.5, 5, 6, or 8°. We added another set of annulus segments confined between iso-eccentricity lines of 3.9 and 4.1°. For all resulting nine combinations of iso-eccentricity lines, polar angle was set at 10, 22, 45, or 90°. Two subjects (PDW and DP) performed five filling-in trials for all 36 resulting annulus segments. A trial lasted for 20 s or until a key press occurred indicating filling-in.

When the data obtained for the different annulus segments (pooled over subjects) were plotted as a function of the smallest distance across the annulus segments' rectangular cortical projections (equal to their shortest edges), the two variables showed a significant, but low, linear correlation ($r^2 = 0.35$, $t = 3.27$, $n = 22$, $P < 0.01$). The linear fit was significantly worse than the one obtained when plotting the data as a function of the square root of projection area ($Z = 2.63$, $n = 22$, $P < 0.01$; compare Fig. 8B and C). Similarly, a significantly worse linear fit was obtained ($Z = 1.97$, $n = 22$, $P < 0.05$) after re-plotting the same data as a function of the distance along the length of the rectangular cortical projection (not shown). Thus, although the linear relation between time to filling-in and square root of projection area initially had suggested to us that it was the shortest distance across the cortical projection area that determined the time required for perceptual filling-in, the present experiment suggests, by contrast, that a more critical factor is cortical projection area per se.

A factor which is strongly correlated with cortical projection area is the total length of the cortical representation of the annulus segment's boundary. As a consequence, we found a strong correlation between the time required to fill-in the annulus segments and the total length of their cortical boundary representation (Fig. 8D). In fact, plotting the data as a function of square root of projection area or as a function of total cortical boundary representation produced linear data fits which were not significantly different ($Z = 1.7$, $n = 22$, N.S.). Thus, either the cortical projection area or the total length of the boundary representation could be the critical factor that determines the time required to fill-in. Additional experiments will be needed to tease the contribution of these and other factors apart.

3.7. Experiment 7: effects of the color of the region to be filled-in

Fig. 9 compares the median time required to fill-in a range of square sizes presented at an eccentrcity of 8°, for both red and gray squares. The data with the red and gray squares were obtained in experiments 5 and 1, respectively (see Fig. 6B and Fig. 1B), and were pooled over subjects. A series of Mann Whitney *U* tests showed for each square size that the difference in the time required to fill-in the red and gray squares was statistically significant ($P < 0.001$). Since the data with the red and the gray square were collected in different groups of subjects, subject PDW replicated the difference in time required to fill-in red and gray squares in a within subject design (unpublished data). The difference shown in Fig. 9 was confirmed. The question then arose whether the quicker filling-in of gray squares would also be correlated with the square's cortical projection area, as we have shown for red squares. To investigate this question, four subjects (MA, PDW, RH and MR) were asked to report filling-in of a gray square in a 16 × 16° texture, viewed from a distance of 35 cm. The square ranged in size from 0.6 to 5.6°, and was presented at eccentricities of 4 or 8°. The stimulus was presented for maximally 12 s. The subjects performed ca. ten trials in each condition.

Figs. 10(A) and (B) show the median time required to perceive filling-in as a function of size, at eccentricities of 4 and 8°, respectively. Fig. 10(C) illustrates the linear fit of the data plotted as a function of square size in visual degrees ($r^2 = 0.53$, $n = 12$, $t = 3.38$, $P < 0.01$) and the solid line in Fig. 10(D) illustrates the linear fit of the data replotted as a function of the square root of cortical projection area in V3 ($r^2 = 0.94$, $n = 12$, $t = 12.62$, $P < 0.001$). The data are fit significantly better by a linear regression after replotting than before ($Z = 2.46$, $n = 12$, $P < 0.05$). The data show that with the gray square, cortical projection area predicts the time required to perceive filling-in, as we demonstrated before using a red square. A given projection area, however, led to slower filling-in when the corresponding square was red than when it was gray, and the difference in filling-in time became more pronounced for larger square sizes (see Fig. 9). This point is further illustrated in Fig. 10(D) by a comparison of the regression lines obtained after plotting the time required to fill-in the red square (stippled line, from Fig. 7B) and the gray square (solid line) as a function of projection area in V3. One possible explanation for this finding is that the red feature competes more with the dynamic texture than does the gray feature, thereby causing an increase in the time required for perceptual filling-in to take place (but see Section 4).

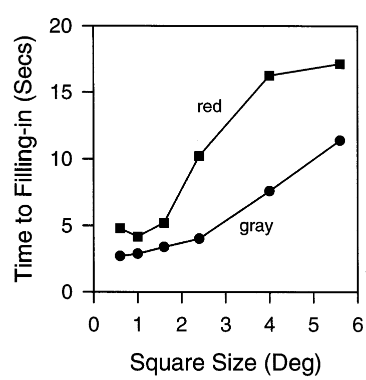

Fig. 9. Median time required for filling-in of a red (solid squares) and a gray square (solid dots) surrounded by a dynamic texture. Same data as in Figs. 6(B) and 1(B), respectively. Red and gray squares were presented at an eccentricity of 8°.

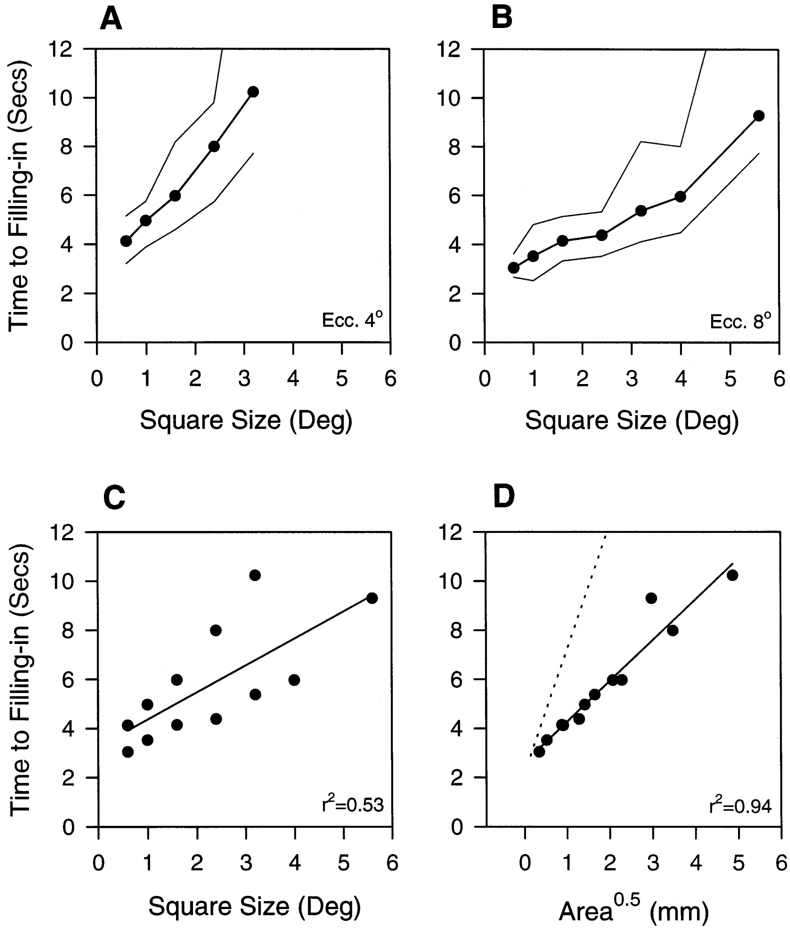

Fig. 10. The relationship between filling-in of a gray square in a dynamic texture and cortical magnification in V3. (A) Median time to filling-in as a function of square size at an eccentricity of 4°. (B) Median time to filling-in as a function of square size at an eccentricity of 8°. Thin lines below and above each data symbol in A and B indicate the 25th and 75th percentile, respectively (pooled data from subjects MA, PDW, RH, and MR). (C) Linear regression through the data points indicating the times required to perceive filling-in plotted as a function of square size, ignoring the fact that the data were collected at different eccentricities. (D) Linear regression through data points indicating the times required to perceive filling-in plotted as a function of the square root of the square's cortical projection area in human V3. The dotted line indicates the regression line obtained with a red square (from upper panel in Fig. 7B).

4. Discussion

It has been known for many years that the perception of stimuli in one part of the visual field is influenced by stimuli in neighboring parts of the visual field (e.g. see refs. [21–24]). In parallel with these psychophysical observations, physiological studies have shown that stimuli outside a neuron's receptive field can inhibit [25–31] or facilitate [28,32,33] responses to stimuli inside its receptive field. Perceptual filling-in is an extreme example of how perception in one part of the visual field can be influenced by stimuli in neighboring parts of the visual field.

In a recent physiological study on rhesus monkeys, we described visual cortical cells whose responses were correlated with perceptual filling-in measured in human subjects [34]. In that study, monkeys maintained fixation while a dynamic texture with a gray equiluminant square in its middle was presented in peripheral vision. After several seconds of stimulation, neurons in V2 and V3 (but not in V1) with their receptive fields centered over the gray square showed strong increases in activity, termed 'climbing activity'. The climbing activity reached an asymptotic firing rate that was similar to the firing rate obtained when a texture was presented inside the receptive field, and the time at which the asymptote was reached correlated well with the time at which human observers reported filling-in with the same stimuli. These results strongly suggest that climbing activity mediates the perception of filling-in.

We proposed in the Introduction that the neural mechanisms causing perceptual filling-in of a gray or colored region surrounded by a large texture during maintained fixation also contribute to filling-in of surface properties during normal surface perception. The perceptual filling-in we studied was much slower, however, than the quasi instantaneous perceptual filling-in of surface properties during normal perception of visual scenes (see ref. [12]). The slow nature of perceptual filling-in with the stimuli used in the present study suggests that the neural filling-in process that forms the basis for perceptual filling-in is slowed down, or delayed, by an antagonistic process which attempts to keep the uniform region segregated from the surrounding texture. Gerrits and Vendrik [10] were the first to propose such an idea, and it has been formalized and extended in a series of theoretical studies by Grossberg and co-workers (e.g. [15,16,35,36]). Gerrits and Vendrik [10] suggested that in normal vision the scope of neural filling-in processes is limited by antagonistic activities that represent boundaries in the image. Under conditions of maintained fixation, however, the boundary representations start to adapt, and filling-in processes spread beyond physically present boundaries. Perceptual filling-in during normal surface perception can occur rapidly because the neural filling-in process can act unhindered to fill-in features between existing boundary representations [12]. Similarly, the fast filling-in of the blind spot may be due to the fact that no boundary representations have to adapt before perceptual filling-in can take place (see ref. [37]). In addition, the possibility exists that a specialized, more hardwired neural mechanism underlies the filling-in across the blind spot [38,39].

In our previous, physiological study of perceptual filling-in [34], we explained our data without assigning a specific role to boundary representations. Rather, we suggested that cells with receptive fields within a gray square embedded in texture receive both excitatory and inhibitory inputs from the receptive field surround, with the inhibitory inputs preventing cells from responding to surround stimuli under normal conditions. Furthermore, we suggested that, over time, the inhibitory inputs would adapt faster than the excitatory ones, thereby allowing previously ineffective excitatory inputs from the surround to become effective in driving the cells. The increased excitatory drive from the surround would lead to the climbing activity which we suggested is the basis for perceptual filling-in.

Related physiological phenomena have been reported by Pettet and Gilbert [40] and by DeAngelis et al. [41]. Pettet and Gilbert [40] stimulated the surrounds of receptive fields in V1 of anesthetized animals with large textures for several minutes and found that the receptive fields increased in size. Recording under similar conditions, DeAngelis et al. [41] also found that V1 cells began to respond better to stimuli outside the classically defined receptive field after prolonged stimulation of the surround, but they interpreted the results as a change in contrast gain rather than a receptive field expansion. The effects on receptive fields in both studies were observed after several minutes, rather than seconds, of stimulation, and it is not known how the spatial extent of these effects compares to the spatial scale of perceptual filling-in under comparable stimulation conditions. It is also not clear if these effects represent a continuation of the rapidly occurring filling-in process in V2 and V3 reported by De Weerd et al. [34]. Furthermore, within the few seconds of stimulation during which perceptual filling-in and climbing activity occurs, De Weerd et al. [34] did not find changes in receptive field size or contrast gain in V3, nor did they find climbing activity in V1 over that time period. Nonetheless, the results found in V1 by Pettet and Gilbert [40] and by DeAngelis et al. [41] demonstrate that the balance between excitatory and inhibitory inputs to V1 cells can change as a result of prolonged stimulation of the surround. It is possible that such a mechanism could contribute to changes in cortical maps after sensory scotomas (see ref. [42]).

Although it seems reasonable to explain climbing activity, and perceptual filling-in, in terms of a fast change in the balance of excitatory and inhibitory inputs from the surround [34], two findings in the current study suggest that the adaptation to the boundary plays an important role in allowing the excitatory inputs to become effective in driving the cell. First, we found that small displacements of a square surrounded by texture significantly delayed or prevented filling-in of the square (see also refs. [3,7]). Second, we found that the total boundary length of the cortical representation of the filled-in region predicts the time required for filling-in, which is consistent with the idea that adaptation to boundaries precedes filling-in. Computational studies have modeled interactions between boundary representations and filling-in processes [15,16,35,36], and have suggested that longer boundaries may require more time to adapt.

In addition to the role played by the length of the boundary, we found that the relative sizes of figure and ground contribute significantly to filling-in. The relative sizes of the texture frame and the enclosed square influenced the time course of filling-in, and determined which region in the image would become filled-in by the other. Furthermore, we found that the time required for filling-in of a gray square in a large texture depended not only on the length of the boundary of its cortical projection, but also on the square's total cortical projection area. The large size and other salient features of a figure can enhance how strongly a figure stands out from its background, which may influence the time course of filling-in. The fact that a red square fills-in slower with the surrounding texture than a gray square supports that idea.

The weak correlation between the time required for perceptual filling-in and the shortest distance across the cortical projection of the filled-in region suggests that the time required for subjects to report filling-in does not reflect a slow spread of a surface feature from one region of the visual field into another. Rather, it reflects the time required for figure-ground segregation to fail, after which a fast neural process allows featural spread of one region of the visual field into another, a process to which we have referred as the neural filling-in process. This neural filling-in process might depend on horizontal connections between pyramidal neurons in extrastriate cortex [43]. Some of our psychophysical findings are in line with the possibility that lateral anatomical connections in retinotopically organized areas are involved in filling-in. We found that there is an upper limit for the gap that can be filled-in by surrounding texture, and we found that adding texture beyond a given frame width does not change the time course of perceptual filling-in. Both findings could be related to the limited span of lateral connections. Optical imaging studies [44,45] have demonstrated fast lateral spread of activation in area V1, and it is possible that similar lateral spread forms the basis of filling-in in extrastriate cortex. The neural filling-in process may reflect a competition between oppositely directed filling-in processes [46], taking place on a fast time scale. Following adaptation of the boundary representation, the time required for the neural filling-in process to fill-in a region in the visual field may depend on the shortest distance across that region's representation (see ref. [12]).

Our findings suggest that the neural mechanisms contributing to perceptual filling-in are localized in retinotopic visual areas. We found that neighboring gray squares in a large texture frequently fill-in at different times. This indicates that filling-in is mediated by mechanisms that operate to a certain extent independently at different retinal locations. We found that variations in the time required to fill-in a region surrounded by texture correlate with variations in cortical magnification within visual areas. Variations in cortical magnification with eccentricity are a hallmark of retinotopically organized visual areas. Thus, our prior finding of a physiological correlate of perceptual filling-in in V2 and V3 [34] is in agreement with the psychophysical results of the current study. We found no physiological correlate of perceptual filling-in in area V1, although we found that relative changes in cortical magnification in V1 can be used to predict the time required for filling-in. Absolute cortical magnification in V1, however, is larger than in extrastriate areas, and it decreases as one moves from V1 to visual areas higher in the hierarchy (e.g. see ref. [20]). If one assumes that this decrease is not accompanied by an equivalent decrease in the length of lateral connections, then it is possible to argue that filling-in does not take place in V1 because the ratio between cortical magnification and the length of lateral connections [47] is too high. In other words, it is possible that filling-in would not occur in V1, because the distance in the visual field corresponding to a typical lateral connection would be too small.

The seconds-long delay before perceptual filling-in illustrates the close intertwining of segregation and neural filling-in processes, which is at the basis of normal surface perception. The interactions between segregation and filling-in processes we studied provide constraints for computational models of filling-in, and set the stage for future physiological experiments aimed at disentangling the various neural processes that contribute to perceptual filling-in.

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Appendix

Each point in each visual field quadrant is determined by an eccentricity and a polar angle. The cortical representation of one quadrant of the visual field can be approximated by an elongated rectangle. Iso-eccentricity lines in a visual field quadrant project as lines parallel to the short side of the cortical rectangle. Points with the same polar angle in a visual field quadrant project on lines parallel to the long side of the rectangle (see ref. [48]). We arbitrarily denote the short side of the rectangle as the X-axis, and the long side as the Y-axis, such that variations of X correspond to variations in polar angle and variations of Y to variations in eccentricity.

Y can be determined from the cortical mapping function. We integrated the equation for the cortical mapping function stated in Sereno et al. [20] which resulted in a function of the form $Y = \{a \cdot \exp[(1-c) \cdot \ln(e-b)]/(1-c)\}$, in which a, b, and c are constants that were optimized for different visual cortical areas. Variable e refers to eccentricity. To obtain an optimal fit of the cortical mapping data shown in Sereno et al. [20], we added an offset term (o), such that $Y = \{a \cdot \exp[(1-c) \cdot \ln(e-b)] - a \cdot \exp[(1-c) \cdot \ln(o-b)]/(1-c)\}$. For area V1, constants a, b, c, and o were set to 20.05, 0.08, 1.26 and 0.36, respectively. For area V3, constants a, b, c, and o were set to 18.28, 0.24, 1.75 and 0.41, respectively.

X is a linear function of polar angle, with $X = w \cdot p/90$, where p denotes polar angle in degrees and w the estimated width of the cortical area. By using cortical magnification (m) functions derived from the cortical mapping function of the form $m = \exp[\ln(a) - c \cdot \ln(b+e)]$, we obtained values of w at an eccentricity of 8° ($w = m \cdot e \cdot Pi/2$) of 6 mm in V3 and 18 mm in V1.

These values are reasonable estimates of the width of the strips of V1 and V3 cortex representing visual field quadrants for eccentricities up to 20° (see flat map of human visual cortex in Fig. 4 of Sereno et al. [20]).

To calculate the cortical representations of the various filled-in regions on the cortex, we used mapping functions representing data in the upper field (see ref. [20]), while our stimuli were presented in the lower quadrant. Although there is no evidence for important differences in the mapping functions of upper and lower fields in V1, the representation of the lower field in V3 is markedly smaller than the representation of the upper field. It is reasonable to expect, however, that the mapping function for the lower quadrant of the visual field in dorsal V3, is a scaled version of the mapping function for the upper quadrant in ventral V3. This is acceptable since cortical mapping functions in different early visual areas are similar, except for a scaling factor to account for their differences in size. This explains why very similar linear fits are obtained when the time required to perceive filling-in is plotted as a function of projection area in V1, or in V3. In addition, the exact value of the estimated width of the cortical rectangle (w) is not critical to obtain the excellent linear fits shown in Figs. 7(B), 8(B), and 11(B). We found similar fits using values of 5, 6 and 9 mm for the width of V3. Using those widths for V3 also did not modify our conclusion from Fig. 8 that the square root of projection area and the total length of the projection area's boundary are better predictors of the time required to fill-in than the shortest distance across the projection area.

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