Effects of Selective Attention on Perceptual Filling-in

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Abstract

After few seconds, a figure steadily presented in peripheral vision becomes perceptually filled-in by its background, as if it “disappeared”. We report that directing attention to the color, shape, or location of a figure increased the probability of perceiving filling-in compared to unattended figures, without modifying the time required for filling-in. This effect could be augmented by boosting attention. Furthermore, the frequency distribution of filling-in response times for attended figures could be predicted by multiplying the frequencies of response times for unattended figures with a constant. We propose that, after failure of figure–ground segregation, the neural interpolation processes that produce perceptual filling-in are enhanced in attended figure regions. As filling-in processes are involved in surface perception, the present study demonstrates that even very early visual processes are subject to modulation by cognitive factors.

INTRODUCTION

Under a variety of conditions, the visual system interpolates information across regions of the visual field where all evidence of that information is lacking, leading to a visual illusion referred to as perceptual filling-in. Perhaps the best-known example of perceptual filling-in is the completion of stimuli across the blind spot, and its underlying neural mechanisms have been described in several physiological studies (e.g., Komatsu, Kinoshita, & Murakami, 2000, 2002; Fiorani, Rosa, Gattass, & Rocha-Miranda, 1992). Filling-in across the blind spot occurs quasi-instantaneously, as is the case also for pathological scotomas (Sergent, 1988; Bender & Teuber, 1946). Furthermore, very fast filling-in (within 80 msec) has been observed across entoptic images of vasculature (Coppola & Purves, 1996). Slower filling-in of retinal images (within a few seconds) has been reported under conditions of artificial retinal stabilization (Yarbus, 1967; Gerrits, de Haan, & Vendrik, 1966; Ratliff, 1958), and during stabilization of peripheral images through maintained fixation (Riggs, Ratliff, Cornsweet, & Cornsweet, 1953; Troxler, 1804). The latter effect is often referred to as the Troxler effect, and the type of perceptual filling-in studied in the present article belongs to this category. The stimulus used consisted of gray or colored figures presented away from a fixation spot on a textured background. In agreement with other studies (De Weerd, Desimone, & Ungerleider, 1998; Ramachandran, Gregory, & Aiken, 1993; Spillmann & Kurtenbach, 1992; Ramachandran & Gregory, 1991), several seconds of continued fixation of the fixation spot led to filling-in of the peripherally presented figures by the surrounding background.

It has been suggested that perceptual filling-in reflects neural interpolation mechanisms that also play a role during normal surface perception (Paradiso & Nakayama, 1991; Gerrits & Vendrik, 1970; Walls, 1954). In particular, during normal vision, inhibitory activity from boundary representations would contain spreading activation related to the perception of surface features. These processes, which would take place in retinotopically organized visual areas, have been formalized in a number of modeling studies (e.g., Neumann, Pessoa, & Hansen, 2001; Grossberg, 1987a). According to this idea, the time before filling-in depends to a large degree on the effectiveness of image stabilization on the retina (see Martinez-Conde, Macknik, & Hubel, 2004; De Weerd, Desimone, & Ungerleider, 1998). Effective stabilization leads to adaptation of boundary detectors, weakening of the inhibitory signal (disinhibition), and spread of surface feature beyond physically present boundaries. Hence, the differences in timing of the various types of filling-in reviewed in the previous paragraph may at least in part reflect differences in effectiveness of retinal image stabilization. The fastest forms of perceptual filling-in (across the blind spot and retinal scotomas) owe their speed to the fact that no boundary representations have to adapt before filling-in can take place.

The time required before perceptual filling-in depends on more factors than just the adaptation of boundary representations. Additional factors include figure size and the length of the figure’s boundaries projected on the retinotopic cortex, the relative sizes of figure and background (Sakaguchi, 2001; De Weerd,
Desimone, & Ungerleider, 1998), and salience of the figure (Stuerzel & Spillmann, 2001; Welchman & Harris, 2001). Furthermore, interactions between local elements in textured stimuli and boundary representations of the figure might modulate the time course of boundary adaptation. In the stimuli used in the present study (Figure 1), the local line elements in the texture might produce an inhibitory effect on neurons that encode the stationary figure boundary. This inhibitory effect might be strong because the line elements are refreshed continuously and the figure boundary is not, thereby contributing to the disinhibition that leads to filling-in (see Francis & Grossberg, 1996; Francis, Grossberg, & Mingolla, 1994).

Fast filling-in of brightness during normal surface perception has been demonstrated with a masking procedure by Paradiso and Nakayama (1991). A number of other experiments confirmed that brightness spread takes place on a time scale of milliseconds for objects that span few visual degrees on the retina (Paradiso & Hahn, 1996; Rossi & Paradiso, 1996; Todorovic, 1987). Biologically plausible, computational models have provided theoretical support for fast brightness interpolation (Neumann et al., 2001; Arrington, 1994; Grossberg & Todorovic, 1988).

Neural signatures of interpolation of brightness and dynamic texture have been reported by Rossi and Paradiso (1999) and by De Weerd, Gattass, Desimone, and Ungerleider (1995), respectively. In the latter study, in rhesus monkeys, activity increases correlating with filling-in were reported in V2 and V3 neurons with receptive fields (RFs) in a gray region surrounded by texture. The data indicated that the activity increases resulted from an adaptation of inhibitory inputs to the neurons with classical RFs overlapping with the figure, such that ordinarily ineffective excitatory inputs from the background in the RF surround became effective in driving these neurons (for review, Tremere, Pinaud, & De Weerd, 2003). The disinhibition preceding filling-in might reflect a slow adaptation of boundary representations and other mechanisms contributing to figure–ground segregation, resulting ultimately in a collapse of figure–ground segregation. The subsequent excit-

![Figure 1](http://www.mitpressjournals.org/doi/pdfplus/10.1162/jocn.2006.18.3.335)
atory response (associated with filling-in) might reflect the spread of the various features in the background texture (in the present stimuli: brightness levels, line elements, texture statistics). Activity traces from individual trials (not shown in De Weerd, Gattass, et al., 1995) show that the onset of excitatory responses can be very sudden (Tremere et al., 2003), suggesting that once disinhibition reaches a critical threshold, a fast neural interpolation response takes place.

It is possible that the interaction between mechanisms of figure–ground segregation and interpolation mechanisms, as well as the spread of different features, is in part carried out by mechanisms in different cortical areas, depending on the features in the stimuli (Gattass, Pessoa, De Weerd, & Fiorani, 1998; Ramachandran & Gregory, 1991). The anatomical substrate of neural interpolation mechanisms is likely to involve horizontal connections (Gilbert & Wiesel, 1989) as well as feedback connections. The fact that long-range horizontal connections have a tendency to connect orientation columns with similar preferred orientations (Gilbert & Wiesel, 1989) may contribute to the perceived similarity of filled-in line texture across the figure and physically present texture in the background.

When more than one figure is presented, filling-in of the figures often occurs at different moments in time (De Weerd, Desimone, & Ungerleider, 1998). This confirms that at least part of the mechanisms underlying filling-in are retinotopically organized (De Weerd, Desimone, & Ungerleider, 1998; De Weerd, Gattass, et al., 1995), and suggests that focused attention might selectively influence filling-in of attended figures (Lou, 1999). A priori, there are at least three ways in which attention might interact with perceptual filling-in. First, attention might delay filling-in (Figure 1A), because attended stimuli have been demonstrated in psychophysical studies to be better detected or processed than unattended ones (Posner, Snyder, & Davidson, 1980), whereas inattention is known to reduce the detection of stimuli (Simons, 2000). Other psychophysical studies have shown that attention can increase the dominance of an attended percept during the presentation of rivalrous or ambiguous displays (Mitchell, Stoner, & Reynolds, 2004; Hol, Koene, & van Be, 2005; Sasaki & Gyoba, 2002; Blaser, Sperling, & Lu, 1999; Tsal, 1994; Brown & Thurmond, 1993; Peterson, 1986). Neurophysiologic data support the idea that the processing of attended stimuli is enhanced at the cost of unattended stimuli (Reynolds, Chelazzi, & Desimone, 1999). Combined, these data suggest that paying attention to a figure should strengthen its figural status, and delay perceptual filling-in by its background. Thus, compared to unattended figures, attended figures would have a lower probability to perceptually fill in first and their filling-in would occur later.

Second, attended figures might fill in earlier than unattended ones as disinhibition resulting from sustained attention (Tremere et al., 2003; Parasumaran, 2000; Freund & Meskanaite, 1992) might add to disinhibition resulting from the adaptation of boundary-related signals (De Weerd, Desimone, & Ungerleider, 1998; De Weerd, Gattass, et al., 1995). Because of the increased total disinhibition for attended figures, neurons with RFs covering the attended figure would become driven earlier by excitatory inputs from the texture background, compared to neurons with RFs covering an unattended figure. Thus, compared to unattended figures, attended figures would have a higher probability of becoming filled-in first, and their filling-in would take place earlier (Figure 1B).

Third, attended figures might enhance the probability of filling-in without affecting the timing (Figure 1C). Attention may simply amplify the effectiveness of both the excitatory and inhibitory inputs from the background texture impinging on neurons with RFs covering the figure, without affecting the balance of excitation and inhibition at any point throughout the adaptation of inhibition. Thus, compared to unattended figures, attended figures would have a higher probability of perceptually filling-in first, but if unattended figures filled-in first this would occur, on average, after the same time as for attended figures. An amplification of both excitatory and inhibitory inputs by attention may produce multiplicative effects on the neuronal responses underlying perceptual filling-in, which, in turn, might produce a multiplicative relationship between the frequency distributions of response times for the filling-in of attended and unattended figures.

The present study was designed to test the above three models of interactions between attention and filling-in. In all experiments, the participants maintained fixation of a central point, while several figures were presented away from fixation on a dynamic texture background. The participants directed attention to the color, shape, or location of one or a subset of the figures, and reported with a button press which figure filled-in first (subjective self-reports). Attended and unattended conditions were analyzed in terms of response timing and frequency. The data are discussed in the framework of input gain models of attention proposed by Desimone and Duncan (1995), formalized by Reynolds, Chelazzi, et al. (1999), and going back to original ideas from Grossberg (1973).

METHODS
Subjects, Setup, and Stimuli
Subjects were college students at the University of Arizona, with normal or corrected-to-normal vision. The subjects in Experiments 1 and 2 participated for credit, whereas subjects in Experiment 3 obtained financial reward. In all experiments, subjects sat comfortably in a chair in front of a computer screen, fixated a red fixation dot in the center of the screen, and pushed a
key on the computer keyboard to signal filling-in of figures presented away from fixation. All subjects were screened by presenting several model trials in the different experimental conditions. During these trials, we ensured that subjects had understood the instructions, and experienced perceptual filling-in. Upon completion of the experiment, subjects were debriefed and informed about the purpose of the experiment. All experiments were approved by the Human Subjects Committee at the University of Arizona.

To ensure a fixed viewing distance of 114 cm, the subjects’ heads were supported by a chin rest. In Experiments 1 and 2, subjects were instructed to fixate. Because of the close proximity of attended and unattended figures (see Figure 1D and E), any systematic fixation errors should have affected the perception of attended and unattended figures equally. In Experiment 3, fixation was monitored using a Microguide Infrared Eyetracker, and trials in which gaze deviated by more than 2.5° from fixation were aborted.

Figures were presented on a background made of dynamic visual texture, which filled the computer screen. All figures (green, red, or gray) were approximately equiluminant with the average luminance of the surrounding dynamic texture (23 cd/m²), were placed at 7° of eccentricity around a central fixation spot, and had a surface area of 2.3° squared (disks, squares, and triangles). The dynamic texture was a movie made of 5 frames, each of which consisted of horizontal, white line segments (0.7° by 0.1°) on a dark background, spaced 0.4° apart on average. Because the position of the line elements was randomized in each frame, playing the movie (at 20 Hz) created a stimulus with continuously jittering line segments. The stimuli were presented for maximally 20 sec. Stimuli were generated with a Number Nine Pepper SGT graphics card, and presented on a color monitor that was set at 480 by 640 pixel resolution and a 60-Hz refresh rate.

Statistical effects were analyzed using t tests, χ² tests, and repeated-measures analysis of variance (ANOVA), in which we assumed sphericity of the data, as more conservative assumptions did not change the outcome of analysis. ANOVA was based on average scores in each condition from each subject. In each ANOVA, there were two main factors (stimulus and attention), and an associated interaction (Stimulus × Attention). The stimulus factor always had two levels [two different (groups of) figures]. Likewise, the attention factor had two levels (attention to one or the other figure, or group of figures).

**Experiments 1 and 2**

In Experiments 1 and 2, stimuli contained six figures, three of which belonged to one set, and three of which belonged to another set (see Figure 1D and E). Subjects started the experiment with a block of trials in which they did not receive an attention instruction. They were merely instructed to press one particular button whenever any of the three stimuli belonging to one set disappeared first, and to press another button whenever any of the stimuli belonging to the other set disappeared first. Because subjects presumably paid about equal attention to both sets of figures, this condition is referred to as the “divided attention condition”. In a second condition, subjects performed the same task, but were instructed to pay special attention to the three figures belonging to one set (e.g., the red disks). In a third condition, subjects were instructed to pay special attention to the three figures belonging to the other set (e.g., the green disks). The order of the latter two conditions was randomized among subjects. The arrangement of shapes was fixed as shown in Figure 1D and E.

Subjects not only pressed one key when they experienced filling-in of at least one object belonging to one set of objects, they were also instructed to press another key when they experienced filling-in of at least one of the other set of objects. Only the first response was used to analyze effects of attention on reports of filling-in. The second response was used to select trials for analysis that would correspond to a reliable time difference in filling-in between attended and nonattended conditions. Trials with two responses that occurred within 500 msec of each other or less (30% of trials) were not included in data analysis.

The analysis of filling-in data in a given condition included trials without a response, trials with a single response, and trials with two responses if the time difference between the two responses exceeded 500 msec. Trials in which the first response occurred within 1000 msec of stimulus onset were excluded from data analysis. After application of these criteria, subjects in Experiment 1 (n = 14) performed 27 valid trials per condition, and subjects in Experiment 2 (n = 18) performed 22 valid trials per condition. Analysis of response times was done after a log-transformation of the data. Reported average response times are based on geometric averages obtained in individual subjects (the exponent of the average of log-transformed response times in individual trials). Because 0% filling-in in a given condition (which occurred in several subjects in Experiments 1 and 2) corresponds to a missing response time in that condition, ANOVA of response times (Figures 2B and 3B) was based on smaller numbers of subjects than ANOVA of percentages filling-in (reflected in smaller degrees of freedom). Including the data from the subjects not included in ANOVA of response times in Figures 2B and 3B did not noticeably change the averages shown. The pooled frequency distribution of response times in Figures 2 and 3 includes all valid trials from all subjects.

**Experiment 3**

In Experiment 3, two gray squares were used as figures, one on the left of fixation, and one on the right.
In a first experiment, six disks were presented peripherally, half of which were red, and half of which were green (Figure 1D). Subjects \((n = 14)\) were instructed to press a designated key on the keyboard the first time any of the red disks disappeared, and to press a neighboring key the first time any of the green disks disappeared. Subjects started the experiment with a block of trials in which they did not receive an attention instruction. Because subjects presumably paid equal attention to both sets of figures, this condition is referred to as the “divided attention condition.” In a second condition, subjects performed the same task, but were verbally instructed to pay “special attention” to the red disks. In a third condition, subjects continued performing the same task, but were instructed to pay special attention to the green disks. The order of the latter two conditions was randomized across subjects (see Methods).

Figure 2A shows that there was a strong bias for green disks to fill in first, irrespective of the attention condition. Nevertheless, compared to the divided attention condition, directing attention to the red disks increased the percentage of filling-in for red disks at the cost of green disks. A converse trend was present when attention was directed to the green disks. ANOVA on percentages of filling-in showed significant main effects for stimulus \([F(1,13) = 59.018; p < .001]\) and attention factors \([F(2,26) = 10.636; p < .001]\). The main effect of attention was due to small differences in the overall percentage of filling-in responses in the three attention conditions. Furthermore, the interaction between stimulus and attention was significant \([F(2,26) = 3.917; p = .035]\). Note that the sum of percentages of trials with filling-in of green or red disks was less than 100 in each condition. This is a consequence of the fact that percentages of trials with filling-in were computed against a total number of trials that also included trials without filling-in (see Methods).

To quantify the effect of attention on the relative frequency of filling-in reports, we computed an attention index (AI), reflecting the average difference in the percent times a set of figures (F1 or F2) filled-in first when it was attended (F1a or F2a) compared to when it was nonattended (F1n or F2n), using the formula AI = \((F1a + F2a) - (F1n + F2n)/2\). This AI equaled 16%, corresponding to a small but significant increase in the percentage of filling-in reports for attended figures compared to unattended figures \((t = 3.037, df = 13, p = .011, \text{two-tailed})\).

Figure 2B shows that despite the trend for a first report of filling-in to correspond more frequently to an attended figure, the response times for filling-in were not influenced by the attention condition. ANOVA showed a small effect of stimulus \([F(1,8) = 5.613; p = .045]\), but the effects of attention \([F(2,16) = 5.613; p = .045]\) and the interaction between stimulus and attention \([F(2,16) = 2.713; p = .097]\) were not significant.

The data indicate that attention increased the probability of filling-in, without affecting the time required for filling-in. This is confirmed by comparing the distributions of response times for individual trials pooled over all 14 subjects for attended and unattended figures (Figure 2C). The distributions were compiled after...
normalization, which consisted in each subject of a division of the log-transformed response time of each trial by the mean of the log-transformed data in attended and unattended conditions combined. Figure 2D was obtained by using each pair of frequencies within each bin in Figure 2C (in attended and unattended conditions) as the coordinates for the data points in the scatterplot in Figure 2D, using the unattended frequencies as $X$ values, and the attended values as $Y$ values. This figure panel shows that multiplying the frequencies of filling-in in the unattended condition with a factor of 1.47 accurately predicted the frequencies of filling-in in the attended condition ($R^2 = .95$).

**Experiment 2: Attentional Selection by Shape**

To replicate the above-described findings using a different kind of attentional selection, and in the hope of avoiding the strong stimulus bias present in Experiment 1, we repeated that experiment using gray disks and triangles as figures (Figure 1E). Except for this difference in stimuli, the experiment was identical to the previous experiment (see Methods). Subjects ($n = 18$) participated in a divided attention condition, a condition in which attention was directed to one type of shape, and a condition in which attention was directed to the other type of shape.

The data in the divided attention condition in Figure 3A show that in the absence of an attention instruction, the first report of filling-in was equally likely to be a disk or a triangle. When attention was directed to the disks, the percentage of responses signaling that disks filled-in first was higher than for triangles, and the converse was observed when attention was directed to the triangles. A significant interaction between stimulus and attention factors [$F(2,34) = 3.928; p = .029$] on percentages of filling-in confirmed the significant effect of the attention manipulation. Expressed with the AI defined in Experiment 1, the effect of attention was 14%, which was significant ($t = 2.688, df = 17, p = .016$, two-tailed), and not different from the 16% reported in Experiment 1 ($t = 0.323, df = 30, p = .748$, two-tailed). The main
factors stimulus \( F(1,17) = .173; p = .683 \) and attention \( F(2,34) = 2.497; p = .097 \) did not reach significance.

Figure 3B shows that there was little effect of attention on the response times associated with first reports of filling-in. ANOVA did show a significant main effect of the attention factor \( F(2,30) = 5.944; p = .007 \), which reflected a tendency for reports of filling-in to occur slightly later in the divided attention condition than in the two selective attention conditions. Possibly, in the divided attention condition, attention may have been spread over all figures and less attention might have been directed to each individual figure compared to the two selective attention conditions, thereby delaying filling-in. According to this reasoning, selective attention to a subset of figures should entail earlier filling-in for the attended figures compared to the unattended ones, which, however, was not confirmed by an interaction between stimulus and attention \( F(2,30) = 0.773; p = .471 \). Thus, we conclude that there was no effect of selective attention on response times. There was also no main effect of stimulus \( F(1,15) = 0.338; p = .569 \).

These data confirm that attention increases the probability of perceptual filling-in, without changing the timing of filling-in. A compilation of the frequency distributions of normalized response times for attended and unattended figures pooled over all 18 subjects supports that conclusion (Figure 3C). As in the previous experiment, multiplying the frequencies of filling-in observed in the unattended condition with a constant factor (1.42 for this dataset) accurately predicted the frequencies of filling-in observed in the attended condition \( (R^2 = .84) \).

Experiment 3: Attentional Selection by Location

Although in the first two experiments, the attention effect was highly significant after pooling over a large number of subjects, the effect was too small to be significant in a majority of individual subjects. In 26 of 32 subjects who participated in the two previous experiments, attention did increase the frequency of filling-in, but a \( \chi^2 \) test \( (p < .05) \) contrasting frequencies of responses in attended and unattended conditions showed that this effect was significant in only six subjects. The present experiment aimed, therefore, to produce a larger attention effect, such that it would
reach significance systematically in individual subjects. We also aimed to test the multiplicative relationship between response distributions of attended and non-attended figures for the anticipated, larger attention effect. To accomplish these goals, we carried out modifications of stimuli and attention task, which also permitted an extension of the previous findings from feature-based to location-based attention.

The stimuli were modified to have only two identical, square figures, one on the left of fixation and one on the right (Figure 1F). In contrast to the previous experiments, this allowed subjects to focus all attention resources on a single figure. Attention was directed to the left or the right figure by means of a tracking task. Subjects ($n=5$) were instructed to report unpredictable physical luminance changes in the attended figure, which occurred, on average, every 2 sec. The subjects were allowed to view these subtle luminance cues in a few pretrials. They were further instructed that the disappearance of any of the two figures signaled the end of the trial and were asked to press the up-arrow key to report that event. Finally, they were instructed to use left- and right-arrow keys to indicate on which side the disappearance occurred (see Methods). Note that the tracking task was portrayed as the main task, and that the instruction did not explicitly ask subjects to pay attention to filling-in.

Figure 4A shows that directing attention to the left strongly increased the percentage of filling-in of the figure on the left compared to the figure on the right, whereas the opposite was true when attention was directed to the right. The effect of attention was confirmed by the significant interaction between stimulus and attention [$F(1,4) = 16.168; p = .016$] revealed by ANOVA on percentages filling-in. There were no main effects of stimulus [$F(1,4) = 0.734; p = .440$] or attention [$F(1,4) = 1.000; p = .374$]. The AI reached 48%, which was significantly different from the 15% obtained on average in Experiments 1 and 2 combined ($t = 2.645; df = 5, p = .046$, two-sided). A $\chi^2$ test on the frequency of filling-in responses showed that this effect was highly significant in all five subjects (all $p$ values below .01).

Figure 4B shows that the direction of attention had no effect on the time required to perceive filling-in. This was confirmed by the absence of a significant interaction between stimulus and attention [$F(1,4) = .064; p = .813$]. Likewise, the effects of stimulus [$F(1,4) = 6.498; F(1,4) = 6.498; p = .046$].

Figure 4C shows that the time required to detect filling-in followed a linear trend. The AI reached 48%, which was significantly different from the 15% obtained on average in Experiments 1 and 2 combined ($t = 2.645; df = 5, p = .046$, two-sided). A $\chi^2$ test on the frequency of filling-in responses showed that this effect was highly significant in all five subjects (all $p$ values below .01).

Figure 4D shows that the direction of attention had no effect on the time required to perceive filling-in. This was confirmed by the absence of a significant interaction between stimulus and attention [$F(1,4) = .064; p = .813$]. Likewise, the effects of stimulus [$F(1,4) = 6.498; p = .046$].

Figure 4. Results from Experiment 3. (A) Percentage of trials in which the left (gray bars) or right (black bars) figure filled in first, under two attention conditions: Attention to the left (Attn L), and attention to the right (Attn R). Error bars are standard errors. (B) Response times of trials with perceptual filling-in (conventions as in [A]). (C, D) Response distributions and their relationship presented following conventions in Figure 2C and D.
distribution of frequencies in the attended condition a multiplicative factor (2.48) was necessary to predict the effect of attention in this experiment, a more elevated time course (Figure 4C). In agreement with the stronger not reach significance.

attention can only be demonstrated with spatially non- to feature attention was likely. Effects of pure feature differed in location from the nonselected figures, and figures based on their features, the selected figures also direct attention to the features or locations of one or this visual illusion (Figure 1C).

The effect of attention on the frequency of perceptual filling-in was observed when observers were cued to direct attention to the features or locations of one or more figures. When the observers directed attention to figures based on their features, the selected figures also differed in location from the nonselected figures, and therefore, a contribution of spatial attention in addition to feature attention was likely. Effects of pure feature attention can only be demonstrated with spatially non-overlapping stimuli (see Treue & Martinez Trujillo, 1999). When the observers directed attention to a figure based on its location, this was done through an arbitrary tracking task, while subjects were unaware that perceptual filling-in was the measurement of interest. The strong effect of attention on perceptual filling-in under these conditions suggests that the attention effect takes place irrespective of the way in which attention is directed to the figure.

Physiological experiments in macaque V2 and V3 suggest that adaptation of inhibition underlies perceptual filling-in. Specifically, recordings of V2 and V3 neurons suggest that a mixture of weak excitatory and inhibitory inputs reaches neurons with RFs overlapping with the gray figure in the texture, and that during maintained peripheral viewing of the figure the inhibitory inputs related to the figure's boundary adapt to permit previously ineffective excitatory inputs from the texture surround to drive the neurons (Tremere et al., 2003; De Weerd, Gattass, et al., 1995). The perceptual consequence of this process is the filling-in of the figure by its background. We propose that attention enhances the mixture of excitatory and inhibitory inputs throughout the entire time course of stimulus presentation, thereby increasing the probability to perceive filling-in in the time period during which disinhibition takes place.

In previous, neurophysiologic studies with briefly presented stimuli, effects of selective attention were demonstrated by the modulation of responses to stimuli presented within the classical RF (e.g., McAdams & Maunsell, 1999; Reynolds et al., 1999; Moran & Desimone, 1985), or by the modulation of the effects of surround stimuli on stimuli in the classical RF (e.g., Ito & Gilbert, 1999; Ito, Westheimer, & Gilbert, 1998), which are related to boundary perception and grouping. In the present psychophysical study, with stimuli stabilized on the retina during many seconds, effects of selective attention were evident in an enhanced probability of perceiving filling-in. We have hypothesized that this finding reflects an enhancement of neural interpolation mechanisms contributing to surface perception, and that the neural mechanism is a strengthening of RF surround influences. A mechanism for the multiplicative modulation of neuronal connectivity, which is a component of an integrative explanation for all the above phenomena, was proposed by Grossberg (1973). Multiplicative modulation of neuronal connectivity was used in several models to explain attention phenomena (Reynolds et al., 1999; Grossberg, 1980), and the same basic ideas of neural connectivity were also used in a theory of boundary completion and surface filling-in (Grossberg, 1987a, 1987b, 1997). Both lines of work have been combined in a detailed model in which specific laminar circuits are used to explain grouping, boundary completion, surface filling-in, and effects of attention on these processes (Grossberg, 1999, 2003a, 2003b; Raizada & Grossberg, 2001; Grossberg & Raizada, 2000). In this model, feedback from layer IV to VI is used

DISCUSSION

We have found that attention increased the probability of perceptual filling-in, without influencing the time required to perceive filling-in. In a given set of trials, attended figures filled-in first more frequently than unattended ones, whereas the average time before filling-in was equal for attended and unattended figures. We did not find support for the idea that attention might strengthen figural status (Figure 1A), which would have delayed filling-in, nor did we find support for the idea that attention might enhance disinhibition, which would have sped up perceptual filling-in (Figure 1B). Instead, attention seems to strengthen the neuronal processes that underlie perceptual filling-in without altering their time course, thereby increasing the probability to detect this visual illusion (Figure 1C).

The effect of attention on the frequency of perceptual filling-in was observed when observers were cued to direct attention to the features or locations of one or more figures. When the observers directed attention to figures based on their features, the selected figures also differed in location from the nonselected figures, and therefore, a contribution of spatial attention in addition to feature attention was likely. Effects of pure feature attention can only be demonstrated with spatially non-overlapping stimuli (see Treue & Martinez Trujillo, 1999). When the observers directed attention to a figure based on its location, this was done through an arbitrary tracking task, while subjects were unaware that perceptual filling-in was the measurement of interest. The strong effect of attention on perceptual filling-in under these conditions suggests that the attention effect takes place irrespective of the way in which attention is directed to the figure.

Physiological experiments in macaque V2 and V3 suggest that adaptation of inhibition underlies perceptual filling-in. Specifically, recordings of V2 and V3 neurons suggest that a mixture of weak excitatory and inhibitory inputs reaches neurons with RFs overlapping with the gray figure in the texture, and that during maintained peripheral viewing of the figure the inhibitory inputs related to the figure's boundary adapt to permit previously ineffective excitatory inputs from the texture surround to drive the neurons (Tremere et al., 2003; De Weerd, Gattass, et al., 1995). The perceptual consequence of this process is the filling-in of the figure by its background. We propose that attention enhances the mixture of excitatory and inhibitory inputs throughout the entire time course of stimulus presentation, thereby increasing the probability to perceive filling-in in the time period during which disinhibition takes place.

In previous, neurophysiologic studies with briefly presented stimuli, effects of selective attention were demonstrated by the modulation of responses to stimuli presented within the classical RF (e.g., McAdams & Maunsell, 1999; Reynolds et al., 1999; Moran & Desimone, 1985), or by the modulation of the effects of surround stimuli on stimuli in the classical RF (e.g., Ito & Gilbert, 1999; Ito, Westheimer, & Gilbert, 1998), which are related to boundary perception and grouping. In the present psychophysical study, with stimuli stabilized on the retina during many seconds, effects of selective attention were evident in an enhanced probability of perceiving filling-in. We have hypothesized that this finding reflects an enhancement of neural interpolation mechanisms contributing to surface perception, and that the neural mechanism is a strengthening of RF surround influences. A mechanism for the multiplicative modulation of neuronal connectivity, which is a component of an integrative explanation for all the above phenomena, was proposed by Grossberg (1973). Multiplicative modulation of neuronal connectivity was used in several models to explain attention phenomena (Reynolds et al., 1999; Grossberg, 1980), and the same basic ideas of neural connectivity were also used in a theory of boundary completion and surface filling-in (Grossberg, 1987a, 1987b, 1997). Both lines of work have been combined in a detailed model in which specific laminar circuits are used to explain grouping, boundary completion, surface filling-in, and effects of attention on these processes (Grossberg, 1999, 2003a, 2003b; Raizada & Grossberg, 2001; Grossberg & Raizada, 2000). In this model, feedback from layer IV to VI is used

\[ p = .063 \] and attention \[ F(1,4) = 1.088; p = .356 \] did not reach significance.

Thus, as in previous experiments, attention affected the probability of filling-in without interfering with its time course (Figure 4C). In agreement with the stronger effect of attention in this experiment, a more elevated multiplicative factor (2.48) was necessary to predict the distribution of frequencies in the attended condition from the distribution in the unattended condition \[ R^2 = .88 \] (Figure 4D). The results show that the effects of attention on the probability of filling-in can be large, even if there is no explicit instruction to pay attention to filling-in. Carrying out a contrast-tracking task within the figure region appears to have an obligatory “side effect” of influencing perceptual filling-in of that figure by its background. Subjects rated their success on the tracking task as very high, but an inspection of the results on that task showed that they performed at chance level. They appeared unable to distinguish fluctuations in visibility of the figure prior to filling-in from physical luminance changes in the figure. The large effects of the attention manipulation on filling-in, however, indirectly support the subjects’ assertions that they did indeed attend conscientiously to left or right luminance cues as instructed. The data from all experiments combined also suggest that the attention-induced advantage in filling-in occurs irrespective of the way in which the figure is selected by attention (by color, shape, or location).

\[ \text{DISCUSSION} \]

We have found that attention increased the probability of perceptual filling-in, without influencing the time required to perceive filling-in. In a given set of trials, attended figures filled-in first more frequently than unattended ones, whereas the average time before filling-in was equal for attended and unattended figures. We did not find support for the idea that attention might strengthen figural status (Figure 1A), which would have delayed filling-in, nor did we find support for the idea that attention might enhance disinhibition, which would have sped up perceptual filling-in (Figure 1B). Instead, attention seems to strengthen the neuronal processes that underlie perceptual filling-in without altering their time course, thereby increasing the probability to detect this visual illusion (Figure 1C).

The effect of attention on the frequency of perceptual filling-in was observed when observers were cued to direct attention to the features or locations of one or more figures. When the observers directed attention to figures based on their features, the selected figures also differed in location from the nonselected figures, and therefore, a contribution of spatial attention in addition to feature attention was likely. Effects of pure feature attention can only be demonstrated with spatially non-overlapping stimuli (see Treue & Martinez Trujillo, 1999). When the observers directed attention to a figure based on its location, this was done through an arbitrary tracking task, while subjects were unaware that perceptual filling-in was the measurement of interest. The strong effect of attention on perceptual filling-in under these conditions suggests that the attention effect takes place irrespective of the way in which attention is directed to the figure.
to modulate the on-center off-surround mechanisms in layer IV that produce boundaries, and that produce input to surface filling-in mechanisms. This feedback provides access for various higher-order variables (including attention) to influence perceptual processing. Within the framework of this model, effects of attention on perceptual filling-in are entirely expected.

Following Grossberg (1973), the response of a neuron relative to its maximum firing rate is given, in essence, by the ratio between the number of excitatory inputs alone and the combined number of excitatory and inhibitory inputs, and attention to a stimulus can be modeled by a multiplicative increase of both the excitatory and inhibitory inputs associated with that stimulus. According to such input gain model of attention, the multiplicative effect of attention on excitatory and inhibitory inputs produced by a single stimulus in the RF is revealed directly by a multiplicative effect on the neural responses to that stimulus. McAdams and Maunsell (1999), using single bar stimuli of moderate luminance contrast, confirmed this prediction by showing that the orientation tuning curve of V4 neurons measured with attended bars could be predicted from a multiplication with a constant of the orientation tuning curve measured with unattended bars. Although this multiplicative effect of attention is strongest at low and intermediate stimulus contrasts, it is weak or absent at higher contrasts (Reynolds, Pasternak, & Desimone, 2000). Reynolds, Chelazzi, et al. (1999) modeled effects of attention when two stimuli inside a neuron’s RF compete for control over that neuron’s firing rate, and they proposed that the attended stimulus wins the competition, thanks to a multiplication with the same factor of excitatory and inhibitory inputs from the attended stimulus to this neuron. Hence, the biasing signal influencing competition is modeled by a multiplicative increase in gain of all inputs provided by attended, but not by unattended, stimuli in the RF. Taken together, the data suggest that attention acts to boost the response to weak stimuli, which increases the probability to detect and correctly discriminate them (De Weerd, Desimone, & Ungerleider, 2003; Ress & Heeger, 2003; Gallant, Shoup, & Mazur, 2000; Reynolds, Pasternak, et al., 2000; De Weerd, Peralta III, Desimone, & Ungerleider, 1999; McAdams & Maunsell, 1999; Reynolds, Chelazzi, et al., 1999; Schiller & Lee, 1991). The idea of a multiplicative increase in the gain of excitatory and inhibitory inputs can also be used to explain the attention-induced increase in the probability of perceiving filling-in. The data suggest that the time course of the disinhibitory process leading to (neural) filling-in is not significantly influenced by attention, but that attention enhances the excitatory responses during discrete periods of disinhibition, which are associated with perceptual filling-in. This implies that, during disinhibition, inputs generated by stimuli placed outside the classical RF would be treated by attention in the same way as inputs from stimuli placed within the classical RF. When this occurs, after prolonged stabilization of the figure on the retina, the surrounding dynamic texture is perceived as if it were “inside” the RF, and neurons with RFs overlapping with the figure become effectively driven by the surrounding background texture (De Weerd, Gattass, et al., 1995). Thus, the multiplicative effect of attention on the probability to perceive filling-in of a figure on a texture background may be linked with a multiplicative effect of attention on inputs from the texture background to extrastriate neurons whose RFs overlap with the figure.

The finding that the timing of filling-in responses is independent of attention suggests that the disinhibition process that leads to neural interpolation takes place irrespective of the presence of attention. Thus, we propose that neural interpolation takes place for unattended figures as frequently as for attended figures, but as soon as figure-ground segregation fails and neural interpolation starts, neural interpolation responses might be stronger when they are enhanced by attention. A physiological study in which neurons would be recorded with RFs in attended and unattended regions might find, therefore, that in the unattended figure region there would be frequent occurrences of neural interpolation responses that would not be associated with a report of perceptual filling-in. By contrast, neural interpolation responses in the attended figure region would be associated more systematically with perceptual filling-in responses. Hence, the smaller probability of perceptual filling-in of unattended figures, therefore, may not reflect a more frequent absence of neural interpolation responses in the unattended figures, but comparatively weaker ones, leading to reduced detection rates, similar to the fact that physically present stimuli can also remain undetected if attention is not directed to them (see Introduction).

From the previous reasoning, the question arises whether the subjective experience of perceptual filling-in is more vivid when it is detected in an attended figure than in an unattended figure. Neurophysiologic studies indicate that the effect of attention to a stimulus is comparable to the effect of a contrast increase. When a stimulus is shown alone in an RF, directing attention to that stimulus produces an increase in the neuronal response similar to the response increase produced by a contrast increase (Reynolds, Pasternak, et al., 2000; McAdams & Maunsell, 1999). When multiple stimuli are shown inside an RF, directing attention to a target stimulus causes this stimulus to dominate the response of the cell, similar to the response dominance acquired by a target stimulus whose contrast has been increased (Reynolds & Desimone, 2003). Furthermore, Carrasco, Ling, and Read (2004) have used psychophysical methods to demonstrate that attention indeed enhances the perceived contrast of visual stimuli. Hence, attention may render the experience of filling-in stronger, and in the absence of attention, this illusion might be weaker.
It could be questioned whether filling-in could be perceived at all in the absence of attention. De Weerd, Desimone, and Ungerleider (1998) showed that in the absence of an attention instruction, neural interpolation can take place at different times for different figures. Because in the present study selective attention to one of two (sets of) figures did not modify the average timing of perceptual filling-in, differences in the timing of perceptual filling-in of the simultaneously presented figures on individual trials did not reflect attention effects either. Neural interpolation in attended and unattended figure regions could therefore have taken place simultaneously, or not, irrespective of the direction of attention. We hypothesize that on trials with (quasi) simultaneous neural interpolation, the illusion will most likely have been perceived (and reported) for the attended figure, because of the attentional enhancement of the neural interpolation response across attended, but not unattended, figure regions. Filling-in of an unattended figure might have been perceived more likely when the neural interpolation of that figure occurred in the absence of neural interpolation of the attended figure(s). Note, however, that in order to evaluate salience of the unattended filling-in percept, an experiment must be designed in which the allocation of attention (away from the unattended figure) is kept constant after the onset of perceptual filling-in.

Our findings show that interpolation processes involved in perceptual filling-in (De Weerd, Desimone, & Ungerleider, 1998; De Weerd, Gattass, et al., 1995) and implied in the normal perception of surfaces (Neumann et al., 2001; Paradiso & Nakayama, 1991; Grossberg, 1987a; Gerrits & Vendrik, 1970; Walls, 1954) are modulated by attention. The present study is in line with other studies that have suggested a role of attention in early visual processes, including visual scene segmentation (Zenger, Braun, & Koch, 2000) and surface interpolation (Hol et al., 2003). Furthermore, perceptual filling-in can be considered as an example of a larger class of contextual effects (Knierim & Van Essen, 1992; Nelson & Frost, 1978, 1985; Westheimer, Shimamura, & McKee, 1976), which are mediated at least in part by horizontal anatomical connections (Stettler, Das, Bennett, & Gilbert, 2002). It has been shown that contextual effects are subject to effects of attention and learning (Gilbert, Ito, Kapadia, & Westheimer, 2000), and our data are also consistent with those findings.

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