Generalized Flash Suppression of Salient Visual Targets

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Summary

A pattern of light striking the retina of an alert observer is normally readily perceived. While a handful of conditions exist in which even salient visual stimuli can be rendered invisible, the mechanisms underlying such suppression remain poorly understood. Here, we describe experiments using a novel stimulation sequence that gives rise to the sudden and reliable subjective disappearance of a wide range of visual patterns. We found that a parafoveal target immediately vanished from perception following the abrupt onset of a surrounding texture. The probability of disappearance was influenced by the ocular configuration of the target and surround, as well as their spatial separation. In addition, suppression was critically dependent upon several hundred milliseconds of stimulus-specific adaptation. These findings demonstrate that the all-or-none disappearance of a salient visual target, which is reminiscent of a high-level selection process, is inextricably linked to topographic stimulus representations, presumably in the early visual cortex.

Introduction

Salient visual stimuli may elude perception even if presented near the center of the visual field. Such invisibility is in some cases brought about by stimulus conditions that disrupt early target representations (Breitmeyer, 1984; Macknik and Livingstone, 1998), while in other cases it is attributed to deficits in visual attention (Driver and Vuilleumier, 2001; Mack and Rock, 1998). Yet, most often, visual suppression cannot be accounted for by purely "low-level" or "high-level" mechanisms (Bonneh et al., 2001; He et al., 1996; Kanai and Kamitani, 2003; Leopold and Logothetis, 1999; Lou, 2001; Mennemeier et al., 1994; Moutoussis and Zeki, 2002; Niedeggen et al., 2002; Pritchard, 1961; Rees et al., 2000; Shimojo et al., 2001; Srinivasan et al., 1999; Thompson and Schall, 1999; Wade, 1978). Instead, research suggests that the contents of perception are ultimately determined by interplay between feature representations in the early cortical areas and processing related to selection and attention at more advanced visual processing stages. Here, we investigate the nature of this interplay, with a focus on how perturbation of a salient stimulus' representation in the early topographic areas might ultimately lead to its complete perceptual suppression.

One well-studied example of suppression is perceptual rivalry, where a visual stimulus offers two mutually exclusive subjective solutions. In *binocular* rivalry, for example, dissimilar patterns shown to the corresponding portions of the two eyes are rarely perceived simultaneously, but instead alternate in their dominance. At each point in time, the nondominant stimulus is invisible (Blake and Logothetis, 2002). An offshoot of this phenomenon, termed flash suppression (BRFS, binocular rivalry flash suppression; Wolfe, 1984), locks the percept in time to an external event, and thereby allows for experimental control over the time course of perception. Specifically, if the two conflicting monocular patterns are presented asynchronously by a few hundred milliseconds (and both remain physically present), the second pattern will dominate perception while the first is completely suppressed. This dominance can last several seconds before the suppressed pattern rises to dominance and normal binocular rivalry ensues. The BRFS paradigm has been a useful tool for electrophysiological studies of perceptual rivalry in animals (Leopold et al., 2003; Sengpiel et al., 1995; Sheinberg and Logothetis, 1997) and, recently, in humans as well (Kreiman et al., 2002).

In the present study, we exploit a novel stimulus that combines principles of BRFS and the recently introduced motion-induced blindness (MIB) (Bonneh et al., 2001), in which salient patterns can spontaneously disappear amidst a moving background. In our paradigm, which we term *generalized* flash suppression (GFS), the sudden presentation of a surrounding pattern after several hundred milliseconds viewing of a salient target results in the target's immediate and sustained disappearance. Unlike BRFS, suppression occurs in the absence of interocular spatial conflict, although we show that it is aided by other types of interocular discrepancy. And unlike MIB, the moment of target disappearance is determined by an external event. Here, we explore the basic properties of GFS, with particular attention paid to the effects of stimulus timing, interocular differences, target content, and surround structure. In the Discussion, we speculate on the underlying neural mechanisms of this phenomenon and compare our results with other forms of visual suppression.

Results

The basic stimulus sequence of GFS is illustrated in Figure 1. Subjects viewed two screens binocularly through a mirror stereoscope. After a few moments of fixation, a target appeared (monocularly in Figure 1) and remained physically present for the duration of the trial. Several hundred milliseconds following target onset, there appeared a surrounding pattern consisting of moving randomly distributed dots (dioptically in Figure 1). Subjects were required to report visibility of the target by pressing buttons (see Experimental Procedures). Following the addition of this second pattern, the target would often appear to vanish, and remain invisible for up to several seconds, leaving a "blank" in the original
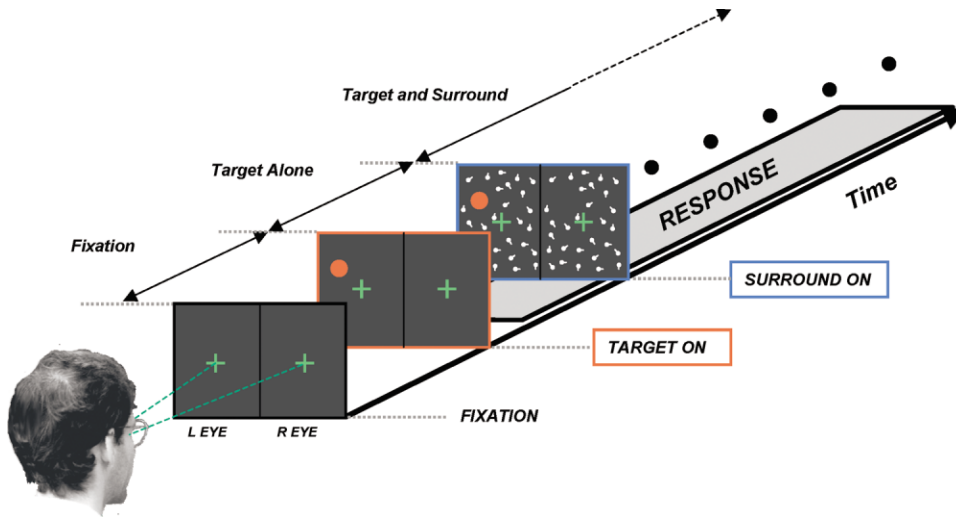
Figure 1. Generalized Flash Suppression Experimental Paradigm Showing Monoptic Target and Dioptic Surround Condition

target position. The blank never "filled in" with surround dots but did adopt the background color. In a typical trial, the subject pressed the button when the target appeared, released it shortly after presentation of the surround (during perceptual suppression), and then pressed it again when the target reappeared.

We first investigated the temporal requirements for the disappearance of the target in GFS in an effort to determine its relationship to other suppression phenomena, such as BRFS and metacontrast masking. Figure 2A shows the resulting probability of disappearance as a function of SOA (stimulus onset asynchrony), for surround dots that were moving (●) or stationary (○). For both surround types, disappearance probability was an increasing function of SOA, with maximal disappearance achieved following roughly 1 s of exposure to the target alone. Disappearance with small SOAs was considerably less frequent, particularly in the case of the stationary dots. The effect of target duration was significant [$F(9,99) = 31.5$, $p < 0.001$], whereas the difference between moving and static dots did not reach statistical significance [$F(1,11) = 2.69$, $p = 0.13$]. These dynamics closely resemble those observed during BRFS (Wolfe, 1984) but differ substantially from the timing requirements for visual masking, where optimal SOAs are generally an order of magnitude smaller (Breitmeyer, 1984; Macknik and Livingstone, 1998).

We next tested the probability of disappearance according to the properties of the target itself. The effect of target eccentricity is shown in Figure 2B, which reveals that although fixated patterns can occasionally disappear (20% of the time for this stimulus), the probability of suppression increased greatly when the target center was a degree or more from the center of gaze [$F(5,20) = 8.25$, $p < 0.001$]. The duration of suppression also increased (data not shown), albeit not significantly, with eccentricity [$F(5,20) = 2.45$, $p = 0.069$]. In addition, Figure 2C shows GFS was effective in suppressing a wide range of patterns. Each plot represents the cumulative density histogram of disappearance times for the different stimuli. Since disappearance latencies are con-

volved with the inherent delays in subjects' responses, we further estimated the true subjective latency by subtracting from these distributions the medians of the reaction time distributions (assessed in separate trials with physically disappearing stimuli). The resulting times, estimating the delay between surround onset and the occurrence of perceptual suppression, ranged in their median between 201 and 291 ms.

We further tested the generality of the GFS effect by asking what types of sudden changes in the surround might instigate target disappearance (Figure 2D). As reported above, stationary dots flashed on the screen, condition (i), were effective in eliciting target disappearance. In the other conditions, the target was placed from the beginning of the trial in the context of a field of stationary random dots. In cases where the dots suddenly started to move (ii), or underwent a color change from white to green (iii), the target tended to disappear immediately on a substantial proportion of trials. This was not the case in the control condition (iv) without any events, in which instances of target disappearance were rare. The removal of the surround pattern never initiated target suppression; however, the sudden freezing of surround motion did sometimes have this effect (data not shown).

Effects of Ocular Configuration

We next investigated the effects of ocular configuration by testing various combinations of monocular and dioptic target and surround (Figure 3). These results show that the highest probability of suppression occurred when the target was shown only to one eye and the surround was shown either to the opposite eye alone or to both eyes in correspondence. This appeared to result from a combination of two factors. First, the target disappeared more frequently when it was presented monocularly rather than binocularly. And second, the presentation of the surround to the other eye (opposite the target) was more effective than presentation of the surround to the target's eye alone. Dioptic presentation of the surround did not interfere with the latter effect
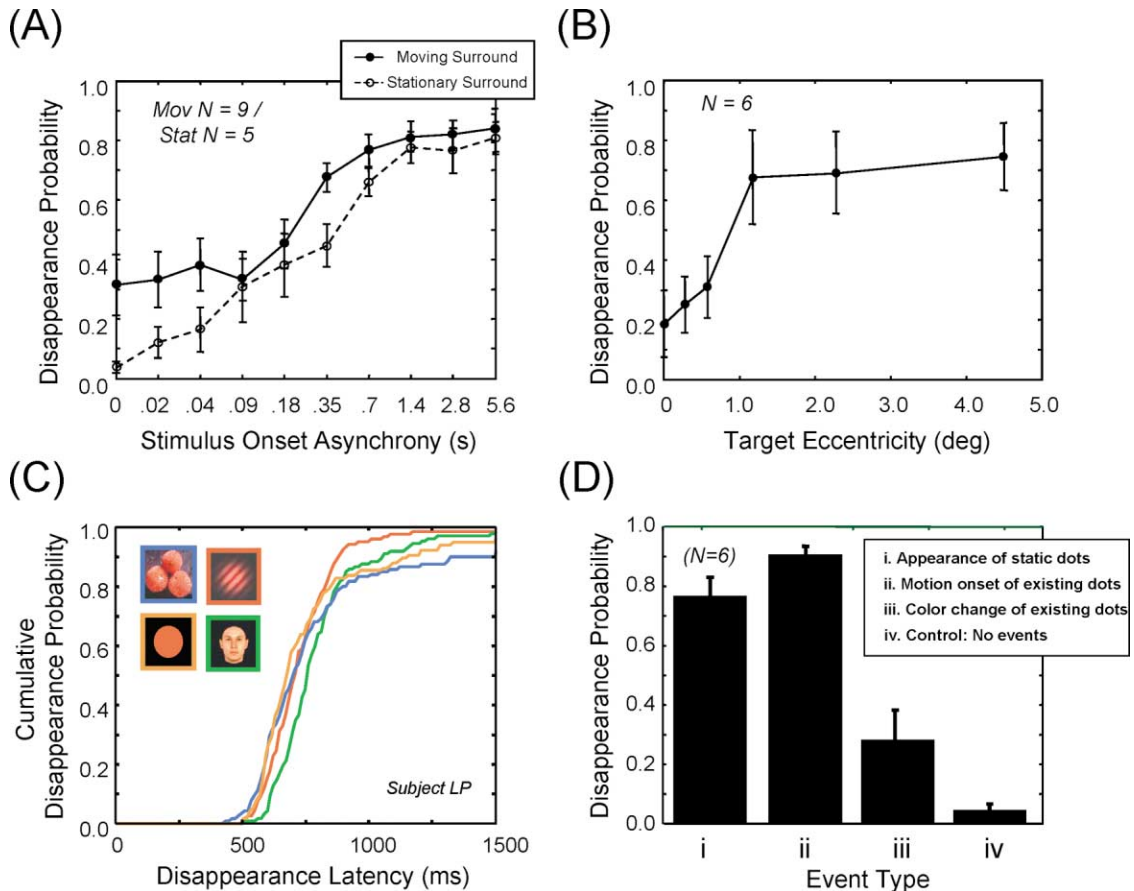
Figure 2. Properties of Generalized Flash Suppression

(A) Effect of stimulus onset asynchrony on the probability of disappearance for moving (●) and stationary (○) surround patterns. The following stimulus parameters are the defaults used in this study, unless otherwise mentioned. The target was a red disk, with a size (T_{sz}) of 1.0° in diameter. The distance between target and surround (i.e., the "protection zone," PZ) was 0.5°. The target was presented at an eccentricity (T_{ecc}) of 1.4° from the fixation cross in the upper left hemifield. The dot density in the surround (S_{den}) was 1.0 dot/deg², and individual dots moved with a speed (S_{sp}) of 5.4°/sec or 0°/sec, for the moving and stationary conditions, respectively. The surround dot lifetime (S_{life}) was 330 ms.

(B) Effect of target eccentricity on disappearance probability. Eccentricity was varied, with stimuli all in the upper left quadrant (S_{den} = 1.25 dot/deg²; S_{sp} = 9°/sec).

(C) Generality of flash suppression for different target types, in this example a uniform red disk, a face, a natural image, and a Gabor grating (spatial frequency 4 cycles/°). Each curve represents the cumulative probability of disappearance as a function of latency for one of the four different target types. Example data from one subject are shown. (T_{sz} [disk, face, natural image] = 1.0°; T_{sz} [Gabor patch] = 3.0°; S_{sp} = 9°/sec).

(D) Generality of flash suppression for different types of surround changes (see Results).

Error bars indicate ±1 SEM.

but rather appeared to enhance it. Note that in none of these conditions was there binocular rivalry nor any form of spatial conflict. Subjectively, the various conditions were nearly indistinguishable, including the all-or-none quality of the target's appearance; nonetheless, the ocular configuration clearly had a major impact on the *probability* of suppression.

Dot Count and "Protection Zone"

We also examined the critical factors in the surround pattern that determine target disappearance. This was done first by changing the density of the dots but keeping the overall spatial extent constant. The results from this experiment, shown in Figures 4A and 4B, demonstrate that disappearance probability was an increasing function of dot density [$F_{(5,25)}$ = 78.6, p < 0.001]. Higher densities also resulted in decreased latency of target disappearance (subject reaction times are included), as shown in Figure 4C [$F_{(4,20)}$ = 19.3, p < 0.001].

To further investigate the contribution of local spatial interactions, the dot density was held constant and a dot-free "protection zone" (PZ; Bonneh et al., 2001) was inserted between the target and the surround (see Figure 5A). The probability of target disappearance fell off gradually with increasing PZ size [$F_{(4,36)}$ = 41.98, p < 0.001], shown for both moving and stationary surrounds in Figure 5B. Note that, even with large PZs, the target sometimes disappeared, particularly when the surround elements were moving. To test whether PZ size was in some sense the critical factor determining the probability of
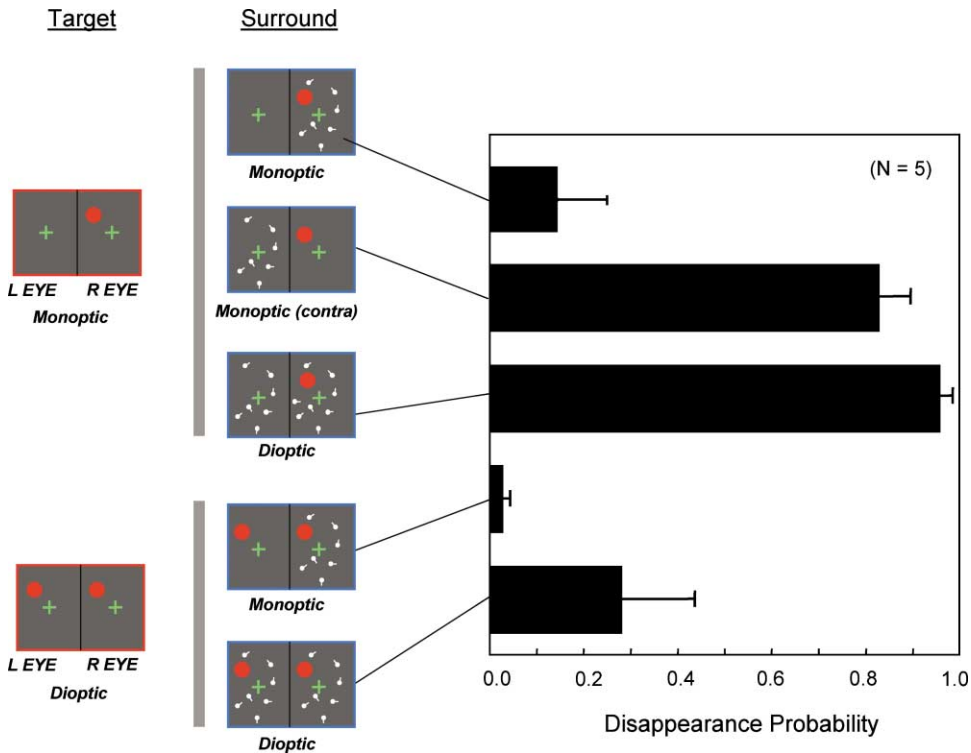
Target   Surround

Figure 3. Disappearance as a Function of Ocular Configuration of Target and Surround

Disappearance probability is shown for five combinations of monocular and dioptic stimulus and surround (S_{den} = 1.25 dot/deg^2; S_{sp} = 5.4°/s or 0°/s). Error bars indicate ±1 SEM.

disappearance, we next varied the target diameter while keeping the PZ constant (Figure 5C). In repeating this for several PZ sizes, we again found an effect of PZ size [$F(2,8)$ = 19.8, $p \leq 0.001$], and a smaller but significant effect of target size [$F(4,16)$ = 7.4, $p < 0.001$], with no significant interaction between these variables ($p > 0.45$). Nonetheless, the relative magnitudes of the two factors shown in Figure 5C reveal that PZ size was domi-

nant in establishing the probability of target disappearance.

The data in Figure 5D show that, as was the case with dot density above, the latency of target disappearance is a function of PZ size [$F(4,20)$ = 19.6, $p < 0.001$]. Previous work has suggested that such latency/distance relationships might stem from propagation delays of a "suppression wave" traveling over topographic vi-
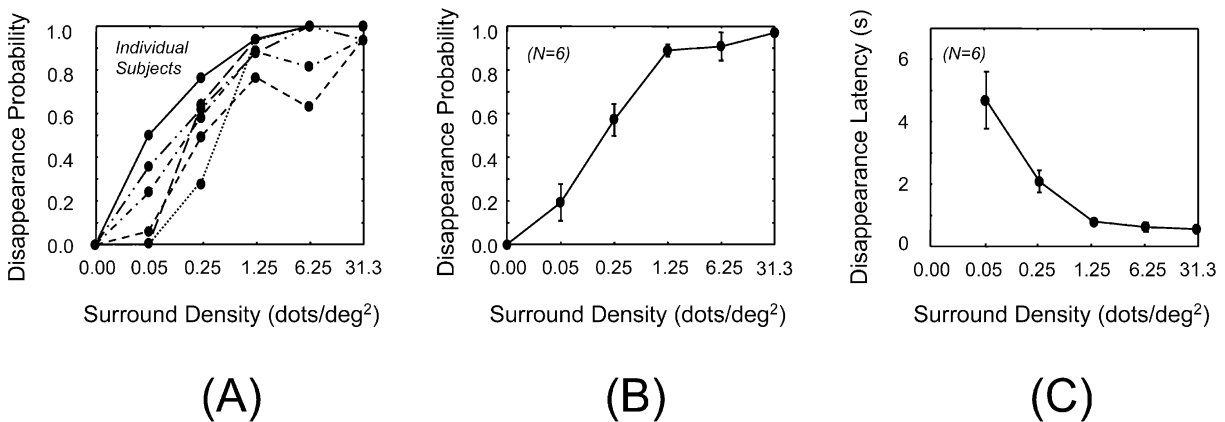

(A)   (B)   (C)

Figure 4. Effects of Dot Density on Disappearance Probability and Latency

(A) Effect of density for individual subjects.
(B) Mean effect of density for six subjects.
(C) Effect of density on the latency of target disappearance.
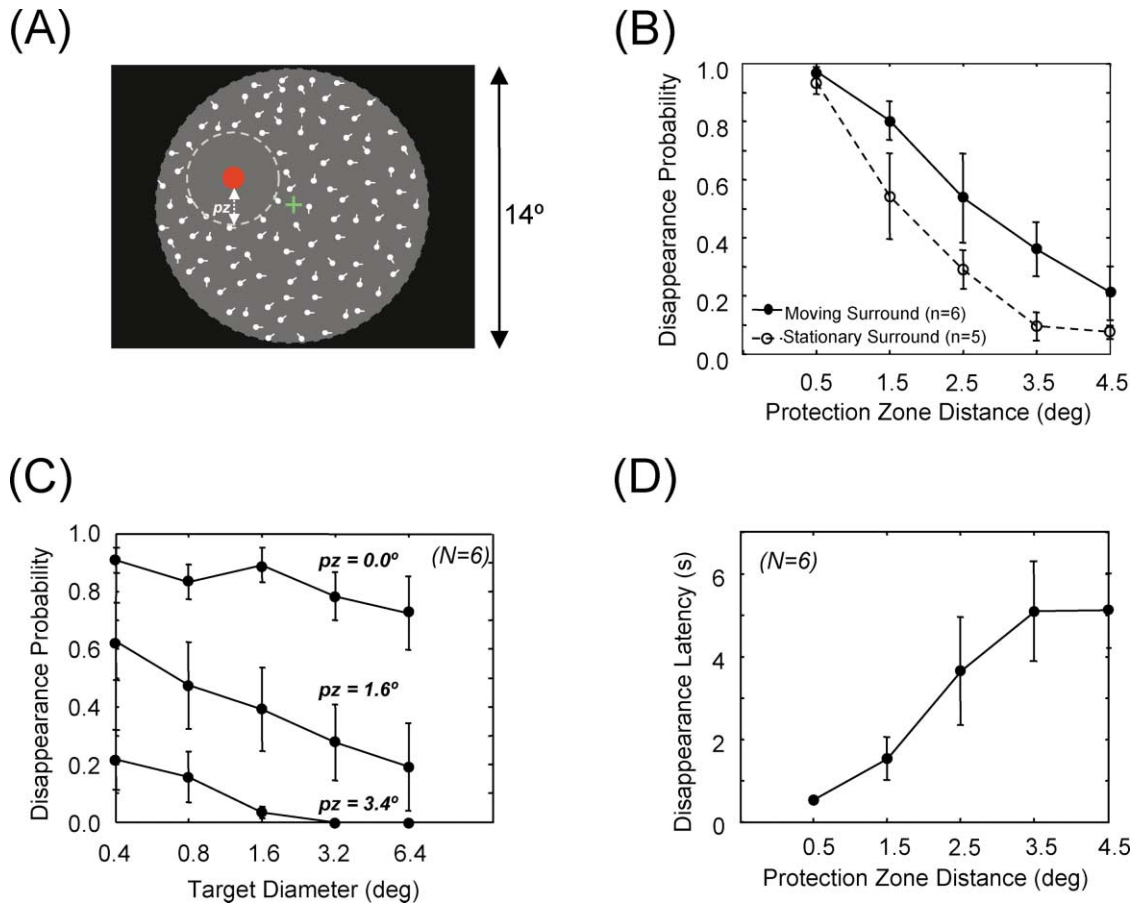Error bars indicate ±1 SEM.

Figure 5. Effect of PZ Size on Stimulus Disappearance

(A) Definition of PZ.
(B) Disappearance probability as a function of PZ size for stationary and moving stimuli (S_{den} = 4.0 dot/deg^2; S_{sp} = 5.4°/s or 0°/s).
(C) Effect of changing the target size but maintaining a particular PZ size.
(D) Effect of PZ size on disappearance latency (T_{ecc} = 2.26°; S_{sp} = 18°/sec).
Error bars indicate ±1 SEM.

sual cortex (see Discussion). To explore this possibility, we designed a stimulus in which the spatial separation was varied between two concentric ring targets (Figure 6A), with subjects reporting the disappearance of each ring using two buttons. If perceptual suppression involves spatial propagation inward from the inducing surround pattern, the outer ring should disappear first, followed after a delay by the inner one. The results in Figure 6B plot the mean *difference* in disappearance times (●, inner minus outer rings) as a function of ring separation. Note that the delays are generally positive valued, indicating that the outer ring consistently disappeared before the inner one. In fact, unlike the inner ring, the outer one nearly always disappeared within a fraction of a second, presumably because of its proximity to the edge of the surround. Also, there is a clear, monotonic trend for longer intervals with increasing separation distance [$F_{(4,16)}$ = 95.28, $p < 0.001$]. Also shown in Figure 6B are the calculated propagation speeds for a theoretical "suppression wave" traveling over V1 (○) for each ring separation (except the two smallest, where the latency difference was shorter than the subjects' reaction time, see Experimental Procedures for details).

Specificity of GFS Adaptation
Finally, given the generality of GFS suppression, its spatial requirements, and the need for a period of exposure or adaptation, we were interested to learn how these various factors might interact. In particular, we were curious how similar the initial "adapting" target must be to the "test" target (when the surround is present) in order for the test target to disappear. The first such experiment, outlined at the top of Figure 7A, examined how a change in position between the adapting and test stimuli influenced GFS disappearance. In the test condition, the screen was blanked briefly (to mask low-level motion transients) after the adaptation phase, and the surround appeared with the target shifted in space (●). The results revealed that even small positional changes (<0.5°) diminished the probability of target disappearance [$F_{(5,20)}$ = 13.3, $p < 0.001$]. In a control condition (○), where the same sequence (including the blank) was used but the initial and final positions of the target were identical (at the test position), the disappearance probability remained high for all target positions. Similar results were obtained when the orientation of a target, rather than its position, was varied (Figure 7B).
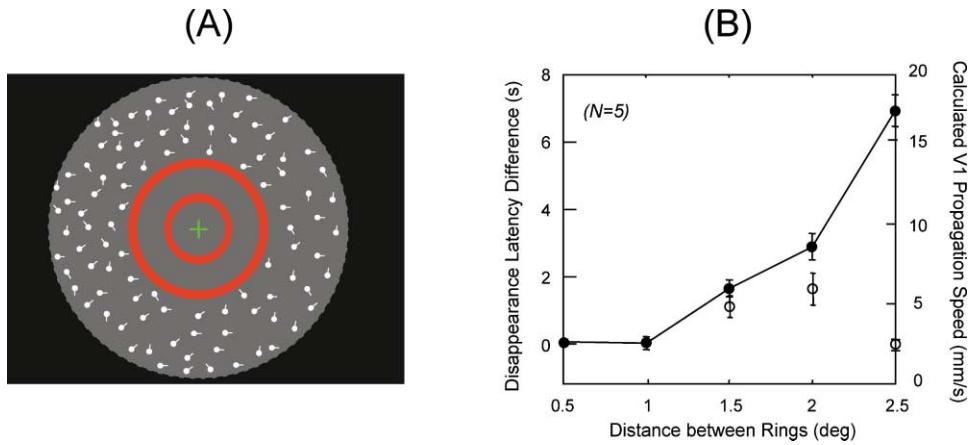
(A)

(B)

Figure 6. Double Ring Experiment to Examine the Spatiotemporal Aspects of Suppression

(A) The stimulus consisted of two concentric rings centered on the fixation point. The diameter of the outer ring was fixed at 7.4°, while that of the inner ring was varied. Each had a width of 0.2°. The gap between the outer ring and the surround (i.e., PZ) was 0.5°.

(B) Time difference between disappearance of outer and inner ring (●). Also plotted is the calculated cortical propagation speed in V1 (○). Error bars indicate ±1 SEM.

Following adaptation with a horizontal bar, testing with an oriented one revealed a limited tolerance for rotation (●), with the probability of disappearance declining significantly with rotations ≥10° [$F(5,20) = 25.6$, $p < 0.001$].

Given that the rotation of a bar could also involve the contribution of small positional changes, we also tested rotation in a Gabor pattern, for which position changes would be minimized. The Gabor results (●) showed a
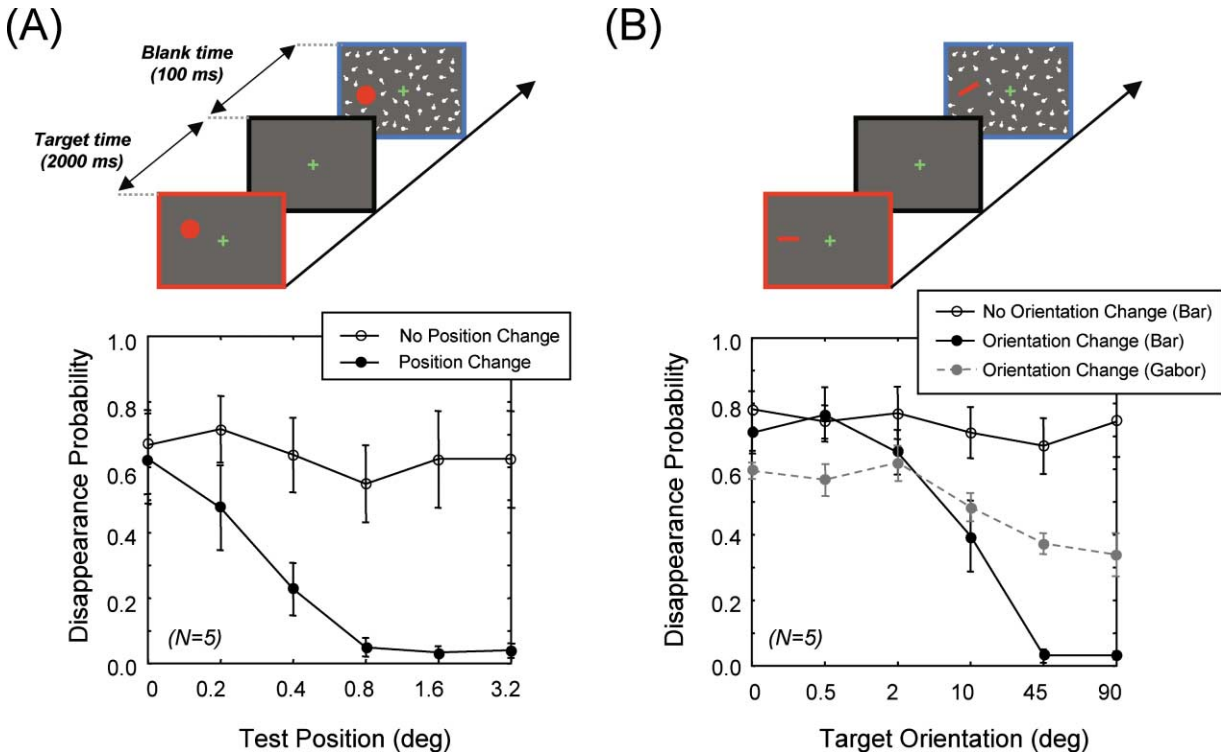

(A)

(B)

Figure 7. Robustness of Suppression to Discrepancies between the Adapting and Test Stimuli

(A) Effect of target displacement for $T_{sz} = 1°$ diameter. In the main condition (●), the adapting target eccentricity was always 1.4°. After a brief blank, the target was shifted horizontally leftward or rightward to the test position (measured relative to the adapting position). In the control condition (○), adaptation and testing positions were the same.

(B) Target orientation. Similar to (A), but the orientation rather than the position was changed. In the main condition, a bar (●), or a 3 cyc/deg Gabor pattern (●) was always horizontal during adaptation and then rotated during testing. In the control condition (○), the adaptation and testing orientation of a bar were the same ($T_{sz} = 0.2° \times 1°$; PZ = 1.8° from target endpoints; $T_{ecc} = 1.8°$ or 2.8°).

Error bars indicate ±1 SEM.

similar trend [$F(5,20) = 8.34$, $p < 0.001$]; however, its magnitude was diminished compared to the bar. The control condition (○) shows that the absolute orientation of the target was not responsible for the observed trends, since the bar disappeared equally at all orientations when the adapting and testing orientations were the same. These results demonstrate that adaptation requirements for GFS are highly specific and suggest that the weakening or disruption of early sensory stimulus representations is critical in obtaining perceptual suppression.

Discussion

A striking aspect of visual suppression is its all-or-none nature. Much of the evidence presented in this paper suggests that the early, topographic visual areas are critical in mediating perceptual suppression. Yet, a diversity of earlier experiments have shown that visual patterns can escape perception despite extensive cortical processing (Blake and Fox, 1974; Blake and Lehmkuhle, 1976; He et al., 1996; Lehmkuhle and Fox, 1975; Leopold and Logothetis, 1996; Logothetis and Schall, 1989; Moutoussis and Zeki, 2002; Niedeggen et al., 2002; O'Shea and Crassini, 1981; Rees et al., 2000; Thompson and Schall, 1999). What follows focuses on how the present findings might provide new insight into how perturbations of early cortical representations are linked to perceptual suppression.

Three Factors Contributing to the GFS Effectiveness

In the present experiments, we showed that three factors contributed, at least to some extent independently, to the perceptual suppression of a target in GFS. Here, we discuss each of these factors, with particular emphasis on how their underlying neural mechanisms might be relevant for determining the visibility of a target.

Target Adaptation
Several hundred milliseconds of adaptation was an absolute requirement to achieve immediate target disappearance in GFS. Moreover, the final experiment demonstrated that the effect broke down when the adapting and test stimuli differed slightly in their position or orientation. These findings implicate early topographic structures, including possibly the retina, as contributing to perceptual suppression. Physiological studies of adaptation in the primary visual cortex have previously shown decreased responsiveness that is stimulus and attribute specific following prolonged sensory stimulation (Carandini et al., 1998; Maffei et al., 1973, 1986; Movshon and Lennie, 1979; Ohzawa et al., 1985). Interestingly, intracellular recordings in this area demonstrated that, following adaptation, stimulus-driven modulation (i.e., input) of neurons was only minimally affected. Instead, the main impact of adaptation was tonic hyperpolarization of the membrane potential, possibly due to decreased efficiency of the predominantly cortical synaptic inputs (Carandini and Ferster, 1997). In GFS, the required period of adaptation may thus act to place target-responsive neurons into such a state of hyperpolarization, ultimately reducing the integration of feedforward signals with recurrent or feedback activity arising from higher cortical processing stages.

Ocular Configuration
In GFS, the target disappeared much more frequently when there was some form of interocular discrepancy. Unlike binocular rivalry, this did not entail direct spatial conflict but was instead most pronounced when the target was monocular and the surround was binocular and in perfect correspondence. In forms of suppression that have both monoptic and dichoptic manifestations, the latter is usually stronger (Andrews and Purves, 1997; Schiller and Smith, 1968). In this respect, the effects of global ocular configuration in GFS are no exception, as mismatches between the eyes increase the probability that the target will disappear. At present, the neural manifestation of such conflict, either local or global, is unclear. While the primary visual cortex (V1) would in some respects be the logical site to mediate such interactions (owing to the large convergence of monocular signals there), some evidence suggests that dichoptic interactions in this area are in fact relatively weak (Macknik and Martinez-Conde, 2000). It is therefore also possible that interocular discrepancies affect more directly mechanisms related to perceptual organization beyond V1 (for a discussion, see Leopold et al., 2003).

Spatial Configuration
The distance between the surround pattern and the target also determined the effectiveness of GFS, suggesting that lateral interactions are important. In previous psychophysical studies, it has been shown that neighboring visual stimuli can either enhance (Kapadia et al., 1995; Polat and Sagi, 1993) or interfere with (He et al., 1996; Intriligator and Cavanagh, 2001; Toet and Levi, 1992) the detectability of a target. In those studies, as well as in the current one, such interactions may be mediated by connectivity in the visuotopic cortical areas (Akasaki et al., 2002; Blakemore and Tobin, 1972; Levitt and Lund, 1997; Sillito et al., 1995; Ts'o et al., 1986). Inhibition may be particularly important since, when measured physiologically, its spatial extent can be an order of magnitude larger than the size of the classical receptive field. Such far-reaching surround interactions might account for the observed effects of both protection zone size and surround density. Interestingly, recent findings suggest that while lateral, intraarea connections may contribute strongly to excitatory reinforcement of basic responses, such as that underlying contour integration (Crook et al., 2002; Stettler et al., 2002), the very large inhibitory portions of the extraclassical receptive field are likely to derive from cortical feedback arising from more advanced processing stages (Angelucci et al., 2002).

The Nature of Visual Suppression

Each factor listed above contributes in its own way to the elimination of a visual target. Importantly, suppression in GFS rarely took an intermediate form, such as giving the impression of a target with diminished contrast. This might be expected if the percept were to draw directly from the strength of sensory responses, weakened by one or more of these factors. Instead, targets were best described as fully visible or fully absent. One possible explanation for this all-or-none quality could be nonlin-

ear or synergistic effects of combining adaptation, surround inhibition, and interocular conflict. If their combined inhibitory effect were to exceed a threshold, sensory responses to the target could be effectively "erased." However, initial neurophysiological findings with GFS have revealed that many neurons in V1 respond to targets that are perceptually invisible (Wilke et al., 2003, Soc. Neurosci., abstract), suggesting that perception does not draw directly from the magnitude of responses in these areas. An alternative interpretation of our results, and that favored by the authors, is that while GFS may exert its primary influence on the early cortical areas, its effects there are more subtle. At present it is only possible to speculate on how perturbing or weakening sensory representations ultimately lead to complete perceptual suppression. One possibility might be that the factors mentioned above disrupt the participation of the target representation in global and recurrent circuits that would normally serve to promote its perception. In this way, the all-or-none perception of a target may reflect the "plausibility" of its sensory representation for higher-level mechanisms of perceptual organization.

In comparing the GFS with other phenomena, it obviously has many properties in common with BRFS and MIB, from which it was derived. For BRFS, this includes nearly identical temporal requirements for suppression (Wolfe, 1984) and its sensitivity to ocular mismatch (albeit a peculiar one). With MIB it shares the lack of a requirement for any local conflict. Interestingly, and in support of the speculations above, neither BRFS nor MIB is thought to arise due to elimination of early sensory responses (Bonneh et al., 2001; Leopold et al., 2003). Recently, a similar phenomenon has been introduced, termed time-locked perceptual fading, in which stimuli can be induced to disappear in a sustained fashion following the onset of a second visual stimulus (Kanai and Kamitani, 2003). Similar to GFS, the probability of disappearance varied as a function of distance between the target and an "inducing" stimulus. Interestingly, briefly extinguishing the target itself could induce its own fading, an effect that was never observed under conditions of GFS. In contrast to GFS, stimuli in that study were presented with high eccentricity (>10°) and viewed under binocular conditions. Further experiments are required to understand the common physiological underpinnings of BRFS, MIB, GFS, and time-locked perceptual fading.

Spatiotemporal Propagation?

The latency of target disappearance increased with large protection zone sizes. It is interesting to speculate that this relationship may emerge because of propagation delays for a wave of suppression traveling over the cortical surface. Recent evidence for this possibility comes from an elegant study of binocular rivalry in which BRFS was used to initiate a visible suppression wave that was then tracked over time (Wilson et al., 2001). In that study, the authors estimated the propagation speed in V1 to be 22 mm/s. Our calculations in the present study led to an estimate of approximately 5 mm/s (see Figure 6). This value is a lower limit since a number of factors, such as the inclusion of delayed spontaneous disappearances, could result in an underestimation.

Similar analysis applied to the perceptual filling in of artificial scotomas in the periphery suggests an even lower propagation speed (0.2–0.6 mm/s) (De Weerd et al., 1998), while studies of brightness filling in of luminance patches probed by visual masking suggest much higher values (150–400 mm/s; Paradiso and Nakayama, 1991).

What might one expect based upon the structure and physiology of the cortex? There is a great deal of evidence that spatiotemporal waves travel over the cortical surface (for a review, see Hughes, 1995). The maximal conduction speed of the neuropil is orders of magnitude higher than that calculated for rivalry or GFS (e.g., propagation of electrically evoked potentials, 1700–2200 mm/s; Freeman, 1959). But many phenomena demonstrate that the cortex is a medium for slower waves as well. Paroxysmal waves in the local field, for example, have speeds closer to those calculated for GFS (60–160 mm/s) (Chervin et al., 1988; Golomb and Amitai, 1997) but are still an order of magnitude too high to explain our observations. On the other hand, cortical spreading depression, of the type associated with visual hallucinations during migraine headaches, propagates much slower (<0.1 mm/s) (Yokota et al., 2002).

Thus, waves of activity can travel with a wide range of speeds over the cortex, including the retinotopic areas, producing a diversity of perceptual correlates. The spatiotemporal organization observed in the current experiments suggests that generalized flash suppression may involve such wave-like propagation, although we remain cautious on this point given that the latency of disappearance also varied with other parameters, such as dot density. And it is important to emphasize that the existence of such waves in perception, even if they do indeed reflect underlying propagation in early cortical areas, do not necessarily imply that suppression is implemented there. They may, for example, instead reflect the need for higher cortical areas to continually reference local feature representations, as well as the topographic layout of the early cortex, in order to achieve the optimal perceptual organization of the input. Such interplay between diverse brain areas may be of great interest not just for artificial suppression phenomena, but for natural vision as well.

Conclusions

What neural mechanisms are then ultimately responsible for the perceptual disappearance of salient stimuli? It is interesting, and perhaps revealing, that despite the large number of experiments that have investigated this question in a variety of paradigms, the answer remains elusive. It is possible that this difficulty stems from the complexity of interactions between stimulus processing in the early cortical areas and perceptual selection at higher stages. For motion-induced blindness, Bonneh et al. likened perceptual suppression to the extinction of salient stimuli experienced by patients with parietal lesions (Bonneh et al., 2001). Such patients, while apparently able to process visual information at a basic level, often completely fail to see salient targets in their contralesional hemifield (Driver and Vuilleumier, 2001; Rees et al., 2000). This sort of high-level "blindness" may play a role in all suppression phenomena, including GFS.

Yet, the current experiments demonstrate that low-level manipulations, directly impacting the early sensory representations, can ultimately govern whether or not a salient pattern is perceived.

Experimental Procedures

Visual Stimuli

Stimuli were generated on a computer (Intergraph Zx10 PC, Huntsville, Alabama; Intense3D Graphics, Sunnyvale, California) and presented on two 21-inch monitors using a mirror stereoscope. The spatial resolution of each monitor was 1,280 × 800 pixels, with an eye-screen distance of 123 cm and a refresh rate of 90 Hz. The visible portion of the screen was seen through a circular aperture with a 14.5° diameter. Both target and surround stimuli were bright and presented on a dark background (CIE: $x = 0.306$, $y = 0.231$, 0.09 cd/m^2). Unless otherwise specified, the following stimulus parameters were used. The target was presented monocularly and appeared alone for 2000 ms prior to the onset of the surround pattern, which was shown dioptically (identical in both eyes). The target was a red disk (CIE: $x = 0.647$, $y = 0.325$, 8.15 cd/m^2), 1.0° in diameter, and presented with an eccentricity of 1.4° in one of four diagonal positions (upper left, upper right, lower left, or lower right, randomly interleaved). The surround was a 10° × 10° square field composed of numerous small white (CIE: $x = 0.321$, $y = 0.317$, 30.1 cd/m^2) dots moving in random directions (dot diameter = 0.08°; density = 1.25 dots/deg^2; dot speed = 5.4°/s; dot lifetime = 330 ms). The surround and target were per default separated by a gap of 0.5°, which was free of surround elements in both eyes and set to the background color (the "protection zone"). A small green plus sign appearing in the center of each screen served as fixation point. The exact stimulus parameters are described in the figure legends of the specific experiments.

Observers

Twenty-four subjects (19 female) between the ages of 19 and 46 (median 23) participated in all experiments in this study. Each subject had normal or corrected-to-normal vision. The number of subjects contributing to each experiment are indicated in the figures. Apart from one of the authors (M.W.) and a technical assistant (O.H.), all subjects were completely naive to the hypotheses and goals of the experiment, gave their informed consent, and were paid for their participation. The experiments were done in accordance with guidelines of the local authorities (Regierungspraesidium). Each subject had normal or corrected-to-normal vision, and most had previously participated in psychophysical experiments. Observers rested their chins on a padded bar and were instructed to maintain fixation on a central cross and to minimize blinking during a trial.

Procedure

Each trial began with the appearance of a fixation cross 1.2 s prior to the target onset and remained visible during the whole trial. The target was then presented for 2000 ms followed by the surround. Subjects indicated the disappearance, and sometimes also the reappearance, of the target by means of a button box. If the target did not disappear and reappear in a 15 s time window, the trial was automatically terminated. Because in some conditions disappearance latency could be quite long, perhaps reflecting spontaneous target disappearance, we restricted much of the analysis to instances of immediate disappearance. In particular, we use the term *disappearance probability* to refer to instances of suppression reported within 1200 ms of surround onset. Although partial or mixed percepts were rare, the subjects were explicitly instructed to consider a target as invisible if and only if there was no trace left and to indicate its reappearance as soon as even the smallest portion became visible.

Subjects were required to maintain fixation throughout the whole trial, although their eye position was not explicitly monitored. Unless otherwise mentioned, the task was to depress and hold a button as long as the target was visible, to release the button when it disappeared, and then to press it again if the target reappeared. All experiments varied parameters in a pseudorandomized fashion. In the different experiments, each stimulus condition was repeated at least 16 times and up to 120. A typical testing block lasted 10–20 min.

Analysis

All relevant events, including stimulus presentations and observer responses, were recorded on a computer for analysis. Data were analyzed using MATLAB (The MathWorks, Inc., Natick MA, USA) and SPSS (SPSS, Inc., Chicago, IL, USA). Unless otherwise specified, statistical analysis relied on computing repeated measures ANOVA, with the within-subject factor being the varied stimulus parameter. Results are expressed in terms of the F ratio, as well as the p value, which was deemed significant if <0.01.

Calculation of the theoretical propagation speed in the double ring experiment employed the formula for the human V1 cortical magnification factor from Engel et al. (Engel et al., 1997),

$$ECC = e^{0.063 \cdot (d + 36.54)},$$

where *ECC* is eccentricity and *d* is the distance in millimeters to the point in V1 corresponding to 10° eccentricity. The cortical position was calculated for each ring, and the speed was computed by dividing the cortical distance by the temporal delay.

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