

# Global competition dictates local suppression in pattern rivalry

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Certain pairs of visual patterns, when superimposed as if transparent, elicit a wavering percept in which one or the other pattern can enjoy temporary periods of exclusive visibility. This multistable perceptual phenomenon is called *monocular rivalry* or *pattern rivalry* (PR) and is most pronounced when the component patterns are faint and devoid of detail. The principal mechanisms that give rise to PR continue to be a topic of speculation. In the present study, we examine the determinants of exclusive dominance during PR using a novel stimulus in which a central portion is free of conflict. By observing the properties of suppression in this so-called rivalry-free region, we demonstrate that perception is driven largely by the global and holistic interpretation of the patterns, rather than by the need to resolve local spatial conflict. The suppression of this central region was often complete and varied as a function of the parameters of the global stimulus, including the size of the surround region, its ocular configuration, and stereoscopic depth ordering. Suppression also varied as a function of pattern continuity across the central region as well as with the temporal offset of the overlapping components. These findings demonstrate that the visibility or invisibility of a pattern is not fundamentally a product of local processing, but is instead shaped by the brain's global interpretive assumptions regarding the composition of the stimulus.

Keywords: multistable perception, perceptual organization, monocular rivalry, visual suppression

## Introduction

Some images, when presented to the visual system in superposition, cause our normally stable perception to waver. Consider, for example, the horizontal and vertical colored stripes shown in combination in [Figure 1A](#). Upon extended viewing of this and similar patterns, an observer will typically notice that one or the other component pattern disappears spontaneously and at times remains invisible for several seconds (Breese, 1899; Campbell & Howell, 1972). This well-known phenomenon is often called *monocular rivalry* to distinguish it from its dichoptic counterpart, *binocular rivalry* (BR); although it is more accurately described by the term *pattern rivalry* (PR), because it can be elicited with either monocular or binocular presentation. Very few patterns give rise to PR involving complete suppression, and they are often regular and repeating patterns, low in both contrast and spatial frequency such as those in [Figure 1](#) (Atkinson, Campbell, Fiorentini, & Maffei, 1973; Campbell, Gilinsky, Howell, Riggs, & Atkinson, 1973; Georgeson & Phillips, 1980; Kitterle & Thomas, 1980; Mapperson & Lovegrove, 1984; O'Shea, 1998; Wade, 1975, but see Boutet & Chaudhuri, 2001). This can be contrasted with BR, for

which nearly any pair of dissimilar patterns, presented to corresponding points in the two eyes, can engage in alternation of complete visibility.

As with most forms of multistable perception, the principal origins of PR remain a point of disagreement and speculation among vision scientists (Andrews & Purves, 1997; Bradley & Schor, 1988; Crassini & Broerse, 1982; Georgeson, 1984; Kitterle & Thomas, 1980; Mapperson, Bowling, & Lovegrove, 1982; O'Shea, 1998; Wade, 1975). There is considerable evidence that adaptation at early processing stages contributes to perceptual suppression. For example, the small displacement of a pattern onto an unadapted region of the retina often disrupts and/or reverses suppression. Early work speculated that such displacements, which occur routinely as a result of involuntary eye movements, may play a causal role in perceptual alternation (Georgeson, 1984; Georgeson & Phillips, 1980; Furchner & Ginsburg, 1978). Other work argues that eye movements cannot fully account for PR phenomena (Andrews & Purves, 1997; Bradley & Schor, 1988; Crassini & Broerse, 1982; Pritchard, 1958; Shimojo, Kamitani, & Nishida, 2001) but nonetheless emphasizes the role of localized processes in the induction and maintenance of perceptual suppression.

Other properties suggest that higher and more cognitive regions of the brain are primarily responsible for the spontaneous perceptual changes observed during PR. Its similarity to other forms of bistable perception, for example, suggests that it participates in a more general scheme for resolving perceptual ambiguity that, although still poorly understood, may involve areas of the brain involved in memory and planning (Kleinschmidt, Büchel, & Zeki, 2001; Leopold & Logothetis, 1999; Lumer, Friston, & Rees, 1998). Comparison of PR with BR in particular reveals a number of common properties regarding the spatial patterns of suppression, dependence on basic stimulus parameters, and temporal dynamics (Crovitz & Lockhead, 1967; Sindermann & Luddeke, 1972; O’Shea, 1998; Wade, 1975). Moreover, PR modulates BR based upon overarching Gestalt principles (Andrews & Purves, 1997). Unlike in BR, where ocular segregation presents a clear basis for competition (because the two eyes see two different patterns occupying the same position in the world), there is no a priori reason that pairs of overlapping images, such as those in Figure 1A, could not be seen stably. Yet, when faced with pairs of “weak” overlapping stimuli, the brain appears unable to maintain a percept that is veridical. The sequences of dominance and suppression, remarkably similar to those observed upon continuous inspection of ambiguous figures, depend on both local and global properties of the patterns, and their initiation is likely to have a central origin (Blake & Logothetis, 2002; Leopold & Logothetis, 1999).

To better understand such central selection processes, the present study set out to examine the balance between local and global processing that determines suppression. We designed a stimulus in which local conflict was present but spatially incomplete, with a central region that contained only one pattern, surrounded by a larger region in which two patterns were superimposed. We demonstrate that the central region regularly and consistently undergoes perceptual suppression, despite the potential for an unambiguous local solution. The quality and extent of this suppression was found to depend upon the diverse characteristics of the conflict outside the window, far away from portions of the pattern that are completely suppressed. We take these results as evidence that visibility across a sizeable portion of a stimulus can be ultimately determined by the brain’s interpretive assumptions regarding its global composition and that perceptual suppression can thereby arise even in the absence of local conflict.

## Methods

### Stimuli

A depiction of the main stimuli used in this study is shown in Figure 1B. This configuration as well as all

other variants used for the study was presented with a size of 10 degrees of visual angle (dva) in diameter (unless mentioned otherwise, the central 4.4 dva were covered by the unambiguous region) and a spatial frequency of 0.5 cycles per degree. Unless mentioned otherwise, stimuli consisted of binocular dim (between 0.62 and 0.97 cd/m<sup>2</sup>) red vertical and green horizontal gratings of sinusoidal luminance profile presented on a black background. (Note that Figure 1 represents a negative version of that stimulus, which was presented on a black background.) Informal observation revealed that different combinations of color and orientation or background color led to similar effects, albeit with varying overall suppression rate (see also Campbell & Howell, 1972; Kitterle & Thomas, 1980; Rauschecker et al., 1973; Wade, 1975, for influence on color on PR, as well as O’Shea, 1998, for an example of a monochromatic PR stimulus). The Michelson contrast varied between 0.4 and 0.5. All stimuli were generated with custom-made software using OpenGL on a personal computer (Intergraph Zx10, Intense3D Graphics) running MS Windows 2000. They were drawn on two synchronized 21-in. CRT monitors, with spatial resolution of 1280 × 800 pixel, an eye–screen distance of 123 cm, and a refresh rate of 90 Hz. Two black apertures surrounding the stimuli presented on a dark gray background helped minimize the occurrence of vergence eye movements.

### Subjects

Forty-seven subjects (36 females) between the ages of 16 and 36 years (median 23) participated in the study (Experiment 1:  $n = 7$ , Figure 2A; Experiment 2:  $n = 10$ , Figure 2B; Experiment 3:  $n = 9$ , Figures 2C and 4B; Experiment 4:  $n = 8$ , Figures 2D, 3A, and 3B; Experiment 5:  $n = 8$ , Figure 3C and 3D; Experiment 6:  $n = 14$ , Figure 4C). Each subject had normal or corrected-to-normal vision, and most had previous experience as psychophysical subjects. All but four (A.M., M.W., M.V., and O.H.) subjects were naïve to the hypotheses and goals of the experiment and were paid for their participation. The experiments were done in accordance with guidelines of the local authorities (Regierungspraesidium), and all subjects gave informed written consent.

### Procedure

Data were collected within sessions lasting 60 to 90 min in a room with reduced ambient light. Each session started with written and verbal instructions, followed by a test trial during which subjects reported subjective and physical disappearances of the central grating. To avoid fatigue, subjects were free to take short breaks after blocks of 5 to 10 min. Each subject rested her or his chin on a padded bar and was instructed to passively inspect the stimulus

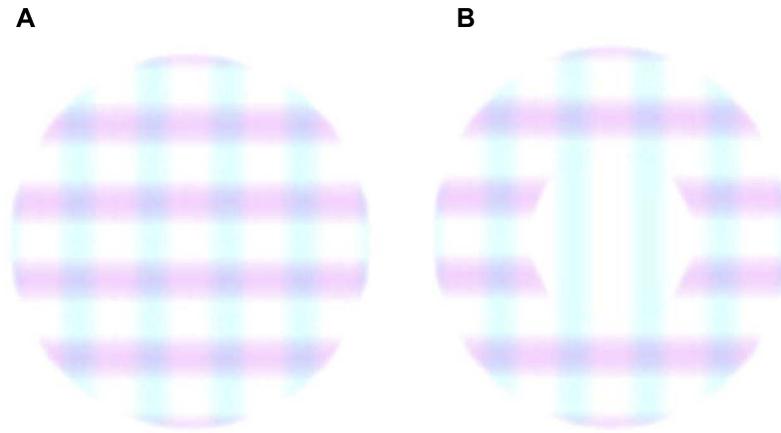


Figure 1. (A). Classical “monocular” PR. Extended inspection of the image may result in alternating perceptions of each of the two gratings in isolation and both of them in superposition. (B). Compound stimulus leading to visual suppression of a large unambiguous pattern region. Although far removed from rivalrous stimulation, visual suppression of the central patch seems to be triggered and coupled to the PR in the periphery. Note that the efficacy of perceptual suppression is highly dependent upon the contrast, and is best viewed on a computer monitor.

presented by a custom-made computer stereoscope. No special regard to eye movements was given because pilot studies revealed no qualitative difference between conditions where subjects were required to fixate and trials where they were allowed to adjust their gaze freely. (When varying a single visual parameter, such as the size of the central portion of the stimulus, similar results were obtained under these conditions, with fixation leading to an overall higher rate of disappearance.) Subjects were required to hold down a button whenever and as long as the central grating disappeared completely. Complete suppression was defined as full replacement of the lines in the central stimulus region by a homogenous field in background color. No attention was paid to any other reductions in stimulus brightness or saliency. This stringent definition of perceptual state has the benefit of being completely unambiguous, but might be partly responsible for the relatively low suppression rates reported in this study. All relevant events, including stimulus presentations and subject responses were recorded on a second computer running under a real-time operating system (QNX Software Systems, Kanata, Ontario, Canada) and stored for off-line analysis.

## Analysis

The data were analyzed using custom software based on MATLAB (MathWorks, Natick, MA). Frequency of disappearance was taken as a measure of suppression because of its high intersubject reliability. Qualitatively similar results were found when total suppression time was considered. Data were normalized by computing each subject’s mean rate and dividing her or his suppression rates for all conditions of this session by this

benchmark value. Note that each session was divided post hoc into one or more experiments as indicated above. Thus, mean rate is not obtained by testing with a standard stimulus, but by referring to the overall rate of suppression each subject experienced on a given day. In addition, lowest and highest absolute mean rates are provided for each figure. (Note that absolute rates in themselves are not an adequate means of comparison because they are known to vary on at least one order of magnitude between subjects for most multistable perceptual phenomena.)

## Results

Figure 1A illustrates the standard paradigm used to induce PR. Observers looking at this pattern for several seconds generally reported spontaneous perceptual alternation between horizontal and vertical stripes. Perceptual suppression ranged from strong contrast reduction to complete disappearance of the nondominant stimulus. To study the local–global interactions, we simply replaced a circular portion of the crossed pattern with the vertical stripes alone (Figure 1B). We reasoned that if PR were driven by local pattern competition, the vertical stripes would dominate this central region regardless of any perceptual changes in the surrounding crossed pattern.

Inspection of Figure 1B reveals that this is actually not the case. Most observers report that when the horizontal stripes are perceptually dominant in the annulus, the center appears blank. In other words, perceptual suppression of the vertical bars was global, including the stimulus parts in the central rivalry-free region. This suppression generally was not accompanied by completion phenomena,

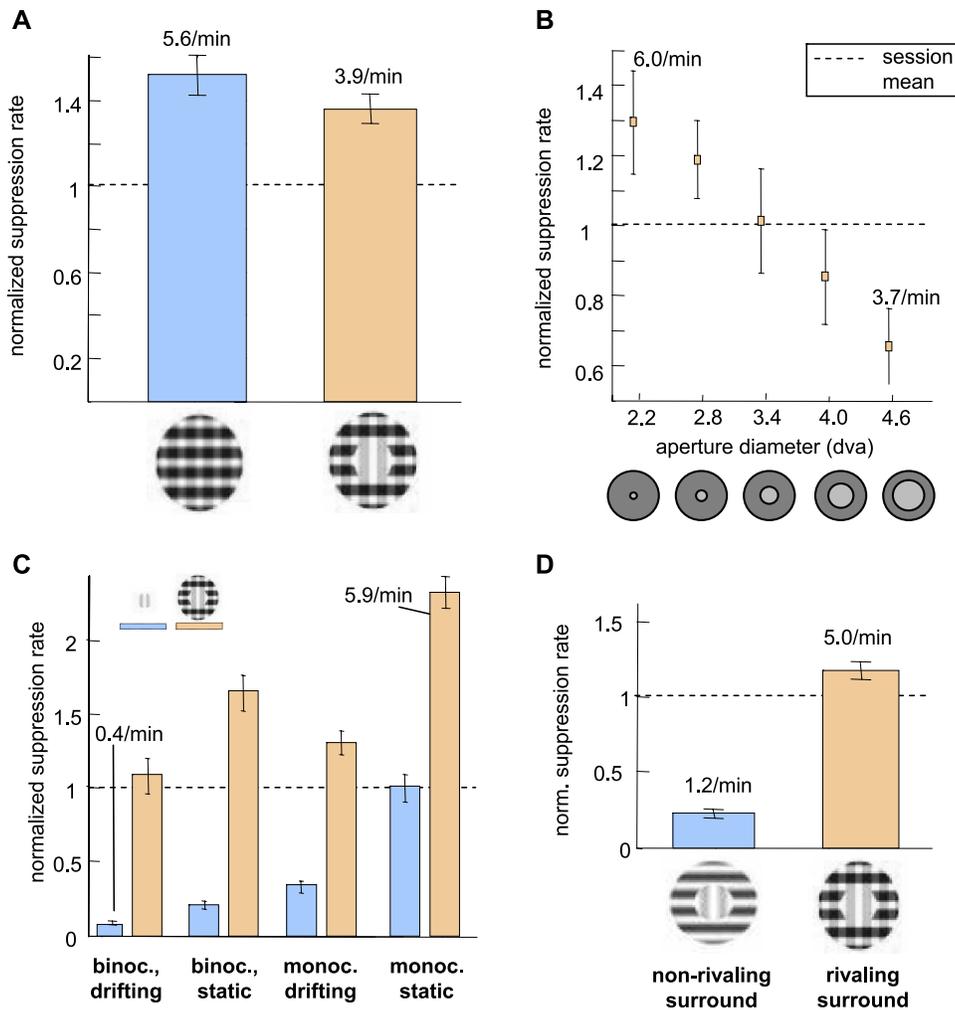


Figure 2. (A). Comparison of the rate of visual disappearance for the complete and partial PR stimuli (normalized mean for seven subjects). (B). Frequency of perceptual alternation as a function of PR annulus size (mean and standard errors for 10 subjects). (C). Comparison of spontaneous subjective fading to cosuppression (mean normalized suppression rate of nine subjects). (D). Assessment of surround effects (normalized mean of eight subjects). Dashed lines indicate mean suppression rate for each session.

such as a “filling in” of the horizontal bars, although faint illusory horizontal lines were reported by some subjects. Foveation of the central region did not prevent pattern disappearance; however, observers often verbally reported their impression that eye movements and blinks tended to interrupt periods of suppression, causing the percept to change abruptly.

We compared the alternation rate for the traditional and “partial” PR stimuli (Figure 2A). Pilot studies revealed that suppression was dependent on the size of the uncompleted central region (Figure 2B). This was true even for stimuli exceeding 10 dva in size, with suppression covering the entire extent of conflicting and conflict-free regions (data not shown). This observation raised the question whether the amount (e.g., area) of conflict determines the rate of perceptual alternation. The results in Figure 2C lend partial support to this interpretation. In this experiment, we tested the spontaneous disappearance of a central patch devoid of visual conflict with and without the surrounding cross

pattern. Faint low-spatial-frequency patterns can spontaneously disappear, particularly if they are presented eccentrically (Troxler, 1804). In this case, we found that a vertically striped patch occasionally disappeared from the center of gaze when presented in isolation, but the frequency of its disappearance was much lower than if the cross-pattern annulus was presented adjacent to it. This was particularly true when the stripes were slowly drifting and presented binocularly. In that case, cosuppression with the rivaling annulus was an order of magnitude more frequent than disappearance of the isolated patch alone. We subsequently confirmed that it was specifically the pattern overlay within the apposed annulus that accounted for the increased central disappearance. Figure 2D shows that the rate of stimulus disappearance significantly declined when the annulus consisted only of the other component pattern, without any rivalry present. Even when we physically alternated the green and red surround components to “mimic” the perceptual transients during

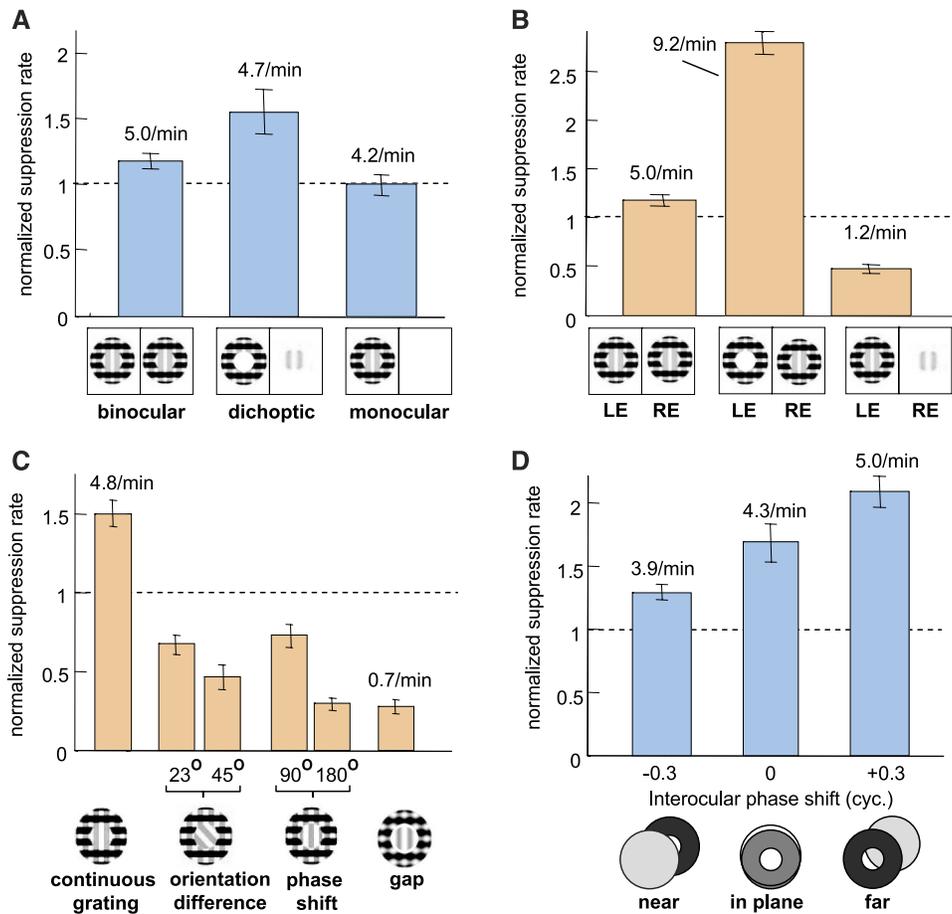


Figure 3. (A). Comparison of suppression rates for the uncompleted patch during binocular, dichoptic, and monocular conditions. (B). Effect of interocular “imbalance” (eight subjects, normalized mean rates). (C). Cosuppression of uncompleted pattern is contingent on perceptual continuity with one of the rival gratings in the adjacent zone of PR conflict. Mean suppression rates for eight subjects are given. (D). Interocular disparity alters suppression probability during PR (normalized mean of eight subjects). Dashed lines indicate mean suppression rate for each session.

PR, we found that suppression was only about half of that when pattern conflict was continuously present (two subjects, data not shown).

Next, given the existence of PR with monocular, binocular, and dichoptic stimuli, we examined under which ocular conditions would disappearance of the central, uncompleted region occur. In Figure 3A, the suppression rate is shown for monocular and binocular conditions, as well as a dichoptic condition where the central patch was shown to one eye and the conflicting surround was shown to the other. In the dichoptic condition, the lack of spatial stimulus overlap successfully prevented the occurrence of classical BR alternation between them. Perception was thus not characterized by an alternation between the two monocular patterns, but instead closely resembled the pattern decomposition observed in the other ocular conditions. We found that the alternation rate for this condition was statistically indistinguishable from the fused binocular and monocular conditions ( $p > .5$ ). Figure 3B shows the effects of other ocular combinations on the rate of central

suppression. For example, when the center was presented to only one eye and the surround was congruent in both, the mean rate of suppression increased by nearly a factor of two. On the other hand, when the central patch was shown to both eyes, but the surrounding crossed annulus was shown to only one, the disappearance rate was roughly half that of the binocular condition. This finding bears a striking parallel to the recently described “generalized flash suppression,” where visibility is influenced in a very similar way by ocular configuration (Wilke, Logothetis, & Leopold, 2003).

Given the observed global nature of pattern suppression, we examined the effects of global continuity of the competing patterns on PR. We varied the phase and orientation of the “uncompleted” stripes in the central portion or introduced a gap between the central region and the PR annulus, effectively breaking the continuity with the similar colored stripes in the rivalrous annulus. The effects of these variables on the frequency of suppression are shown in Figure 3C. The subjects’ spontaneous

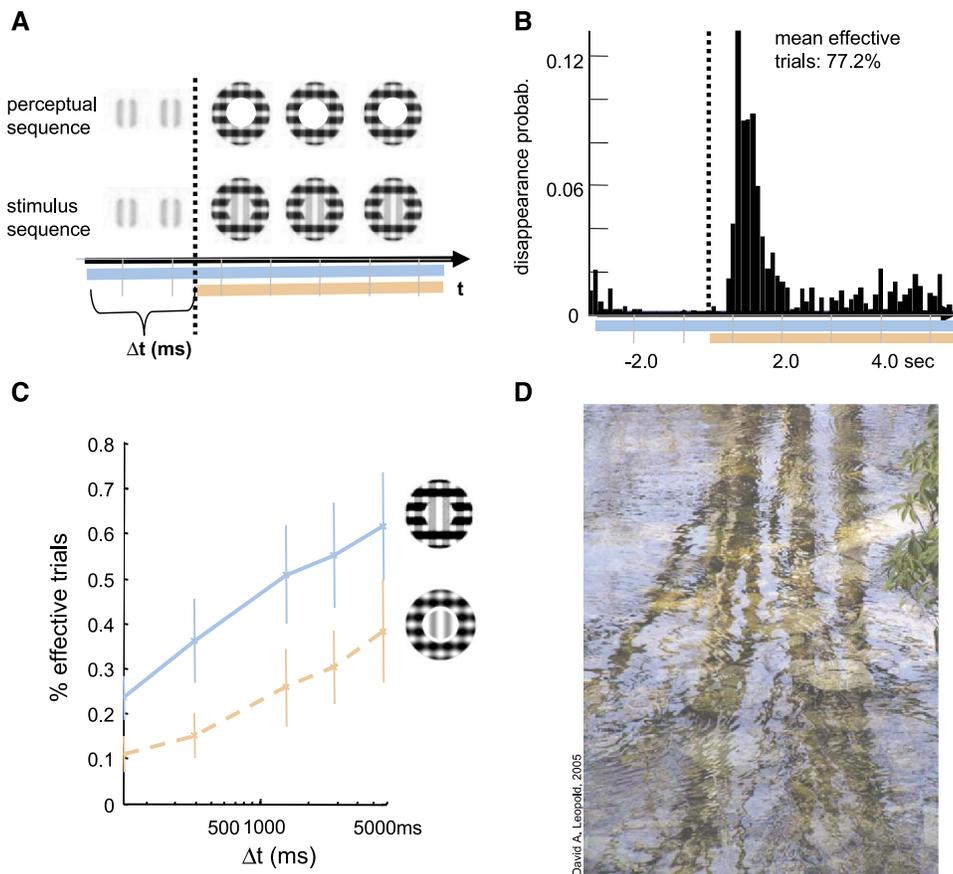


Figure 4. Delayed presentation of surround can trigger disappearance. (A). Stimulus presentation sequence. Central patch was presented for 2.5 s, followed by a sudden onset of the PR annulus. (B). Histogram of disappearance as a function of time (bin size: 100 ms). Each of nine subjects performed 39 subsequent trials (individual histograms were qualitatively comparable). Effective trials are all single runs in which suppression of the central patch was reported after onset of the conflicting patterns. (C). Adaptation time ( $dt$ ) was varied during a 10-min period with pseudorandomized trials of asynchronous stimulus presentation for the complete and interrupted versions of the compound stimulus ( $dt = 44, 354, 1400, 2800, \text{ and } 5600$  ms). Subjects were required to fixate throughout all trials. Mean and *SEM* for 14 subjects are plotted on a log-log scale. (D). Complex stimuli fluctuate in saliency rather than complete visibility.

disappearance rate was found to be significantly lower than that observed with patterns of continuous properties. An increased orientation difference led to a stronger effect, as did the amount of relative spatial shift. Interestingly, the disappearance in the discontinuous case closely resembled that of a patch presented in isolation, again in accordance with predictions of a pattern-based suppression hypothesis.

We next asked whether segregating the competing patterns into different stereo depth planes would significantly alter the pattern of suppression. Such a manipulation might be taken as additional cues for the visual system and thereby aid in resolving the pattern conflict. Disparity-based separation of depth planes is considered a critical contributor in image segmentation (e.g., Nakayama, Shimojo, & Silverman, 1989). If PR is based on implausible sensory evidence for more than one object located at the same position of the visual field (which is also one possible interpretation of BR), then shifting these patterns in the third dimension would disambiguate the stimulus. The

expectation might then be that compatibility of both percepts could be supported and the rate of suppression would subsequently decrease (e.g., Riani, Tuccio, Borsellino, Radilova, & Radil, 1986). Interestingly, we found the largest effect to be a significant increase in the rate of suppression, and this occurred specifically when the vertical grating (including the central, uncompleted portion) was further away in depth than the annulus (Figure 3D). With opposite depth ordering, there was a weaker but reliable change in the suppression rate showing a reverse effect. This finding parallels a recent report of target suppression during motion-induced blindness (MIB) (Graf, Adams, & Lages, 2002). Likewise, it has been shown that temporal asynchronies that aid the visual system in segmenting two overlapping stimuli can increase PR (Suzuki & Grabowecky, 2002). Thus, disambiguation of superimposed patterns in terms of their temporospatial attributes might even enhance their competition, which adds further evidence to the assumption of a global pattern-based origin of this phenomenon.

Finally, we tested the possibility of external triggering of suppression by an asynchronous presentation of the two component patterns. The central patch consisting of the vertical stripes were shown binocularly for 2.5 s, followed by the rivalrous annulus, as shown in [Figure 4A](#). This temporal paradigm is directly analogous to that used to bias perception in BR (Wolfe, 1984) and other (Breitmeyer & Rudd, 1981; Kanai & Kamitani, 2003; Wilke et al., 2003) visual suppression stimuli.

The results, summarized in [Figure 4B](#), show a histogram of reported disappearance times relative to the onset of the annulus. Note that in the majority of trials, the central patch disappeared within 1.5 s, with a strongly diminished probability of suppression afterward. Thus, external onset of visual conflict leads to the suppression of adapted rival components on a global basis. To investigate and verify the role of adaptation for flash-induced PR suppression, we varied the stimulus onset asynchrony between the central patch and the PR annulus. The results of this experiment can be seen in [Figure 4C](#). Increasing stimulus onset asynchrony resulted in a logarithmic rise of suppression probability after onset of the rival pattern, similar in its characteristic to BR (Wolfe, 1984) and generalized flash suppression (Wilke et al., 2003). We found an analogous effect for the stimulus variant that included a physical gap between uncompleted patch and PR surround, however, with a significantly lower absolute amount of suppression probability compared with the complete stimulus.

## Discussion

The stimuli used in the present study demonstrate that there exist significant global determinants of suppression in (monocular) PR. As mentioned, relatively few stimuli give rise to complete suppression in PR, although partial suppression and alternation of “emphasis” are easily demonstrable with more arbitrary overlapping patterns (e.g., [Figure 4D](#) can give the impression of subtle changes in the “saliency” or even depth ordering of two superimposed objects without leading to proper PR). BR, although sharing a number of properties with PR, stands in distinction on these points. Perceptual suppression can arise when virtually any pair of dissimilar stimuli are shown to corresponding regions of the two eyes. Also, the depth of suppression during BR is generally complete (i.e., one of the stimuli is completely invisible at each point in space, without transparency), but its expression is often as a mixed patchwork of dominance between the competing stimuli, typically described as piecemeal (e.g. Blake, O’Shea, & Mueller, 1992). Thus, although global configural factors are known to impact BR as well, perception tends to resolve the conflict in circumscribed (i.e., local) zones of dominance. Careful measurements have demonstrated that, at least for many commonly used

stimulus types, these zones extend roughly  $1^\circ$  from the site of conflict (Blake et al., 1992; Kaufman, 1963; O’Shea, Sims, & Govan, 1997). In the present experiments, windows exceeding  $4^\circ$  in diameter were consistently and uniformly suppressed. It may be informative that such suppression was contingent upon there being strict continuity in the pattern (i.e., stripes) between the window and the surrounding region. This requirement for “good continuity” is suggestive that Gestalt-type principles play a role in the determining what is suppressed. This and other observations, such as the role of depth ordering in suppression, are consistent with the notion that conflict resolution in PR is fundamentally a problem of perceptual organization rather than of exclusively peripheral origin. Although the induction and extent of suppression of BR alternation might be more locally restricted than in PR (Carlson & He, 2004), the global context of a scene alters BR alternation as well (e.g., Alais & Blake, 1998, 1999; Alais, O’Shea, Mesana-Alais, & Wilson, 2000; Fukuda & Blake, 1992; Paffen, te Pas, Kanai, van der Smagt, & Verstraten, 2004). Similarly, contextual factors can modulate the pattern of spontaneous disappearance during MIB (Bonneh, Cooperman, & Sagi, 2001; Graf et al., 2002). All these phenomena are thus likely to be part of a more general phenomenon of spontaneous perceptual reorganization that is not restricted to the subjective elimination of parts of the visual scene (Leopold & Logothetis, 1999).

The main finding of the present study that suppression is manifested globally seems to point to the contribution of “higher” cortical structures. Areas such as the inferotemporal cortex in primates, for example, are often considered to be involved in holistic stimulus processing (Logothetis & Sheinberg, 1996). Yet, it must be noted that most studies on PR to date have used low-contrast sinusoidal grating patterns (Atkinson et al., 1973; Kitterle & Thomas, 1980; Mapperson & Lovegrove, 1984; O’Shea, 1998), which are suboptimal for activating neurons in the inferotemporal cortex. Interestingly, when more complex patterns or images are superimposed, such as in [Figure 4D](#) (in this case, the reflection of a tree on a creek’s water surface), exclusive visibility is seldom achieved (but see Boutet & Chaudhuri, 2001), suggesting that activation of higher object-processing areas may even serve as a hindrance for achieving complete perceptual suppression during PR. This is noteworthy, because this is decisively not the case for BR. Future research will be needed to delineate the effect of stimulus type on perceptual rivalry.

It is clear that some degree of image stabilization on the retina appears to be important for PR. Adding a slow drift to low-contrast gratings does not completely disrupt PR, albeit it does diminish it. The role of adaptation may relate to the well-known observation that most visually responsive neurons reduce their response rate over time upon extended exposure to the same stimulus, an adjustment

that is thought to involve both inherent cellular (Sanchez-Vives, Nowak, & McCormick, 2000) and intracortical network processes (Carandini, Barlow, O’Keefe, Poirson, & Movshon, 1997). This implies that the impact of a stimulus after several seconds of strict fixation is considerably reduced compared with the time of its initial presentation. In the case of PR, this diminished activity might further weaken an already frail representation. Thus the effect of adaptation may be leading to an output to higher areas that is imperceptible or implausible, making it more susceptible to suppression. Although this model might reconcile the necessity of local adaptation with suppression by global conflict, it is important to keep in mind that complete suppression (i.e., invisibility) during PR seems to be the exception rather than the rule.

It is interesting that with stimuli such as that in Figure 4D, a fixating observer will typically notice a familiar dynamic that in some ways resembles PR alternation. This observation raises the possibility that the core processes of PR are not fundamentally linked to stimulus visibility per se, but may instead be ubiquitous, escaping our introspection (Leopold, Maier, Wilke, & Logothetis, 2004). Recent findings indicate that visual attention can express itself in a measurable boost of a stimulus’ apparent contrast (Carrasco, Ling, & Read, 2004). An established attention-induced salience increase can even transfer across space in a feature-selective manner (Rossi & Paradiso, 1995). Moreover, it has been shown that attracting attention to one of two patterns shown in superposition will strikingly increase the probability of this pattern’s dominance during ensuing rivalry (Mitchell, Stoner, & Reynolds, 2004). In this vein, faint low-spatial-frequency grating patterns may serve as a standard PR stimulus because they are an optimal, highly sensitive probe for measuring a more general dynamic process related to the continuous redistribution of attention. Only when such faint probe stimuli are further weakened by localized adaptive processes do global attentional fluctuations appear as noticeable changes in the visual percept (see also Wilson, Krupa, & Wilkinson, 2000).

On a more speculative level, perceptual (monocular) rivalry may be more closely related to our normal vision than previously appreciated (but see Andrews & Purves, 1997). A background, behind the point of focus, tends to cast a blurred image onto the retina. By implication, the neural processing of a steady ambient background may be fundamentally different from that of more relevant visual information in the foreground (Baumann, van der Zwan, & Peterhans, 1997; Heider, Meskenaitė, & Peterhans, 2000; Wong & Weisstein, 1982, 1983). Although the same portions of the primary visual cortex would need to deal with both types of processing, it might be that different “modes” of processing might occur within the same structure—one highly detailed and local and the other coarse and global. With regard to the latter, it is conceivable that the brain strives to maintain a plausible representation of the background without con-

tinually reevaluating the details of the visual input (O’Regan & Noe, 2001). Neurons in the primary visual cortex and neighboring areas are thought to mainly be involved in feature analysis. Yet, there is increasing evidence that activity in these retinotopically organized areas serves various purposes beyond simple identification of border features (Lamme, 1995; Li, 2002; Tehovnik, Slocum, & Schiller, 2003), such as information about the ultimate depth ordering (e.g., figure vs. background) of stimuli (Lamme, 1995). This indicates that some aspects of the global scene organization are present (and hence available) at the earliest cortical processing stages. The global suppression observed in the present study may be explained by neurons in the topographic areas that define a coherent and singular context or reference to serve as a backdrop for the analysis of objects and events in the immediate focus of scrutiny (Baumann et al., 1997; Heider et al., 2000).

In most situations, the unambiguous and stable world justifies this perceptual shortcut. However, when the structure of a scene poses a perceptual challenge, the brain is forced to gamble with a given solution, and this solution must be conceived and implemented on a global level. A coarse but strictly topographic representation of the world may ensure moment to moment registration of events, aid in perceptual continuity surrounding blinks and eye movements, and contribute to our vivid impression that we are continually experiencing the background, even if it is out of our focus of attention.

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## References

- Alais, D., & Blake R. (1998). Interactions between global motion and local binocular rivalry. *Vision Research*, 38, 637–644. [PubMed]
- Alais, D., & Blake, R. (1999). Grouping visual features during binocular rivalry. *Vision Research*, 39, 4341–4353. [PubMed]

- Alais, D., O’Shea, R. P., Mesana-Alais, C., & Wilson, I. G. (2000). On binocular alternation. *Perception*, *29*, 1437–1445. [PubMed]
- Andrews, T. J., & Purves, D. (1997). Similarities in normal and binocularly rivalrous viewing. *Proceedings of the National Academy of Sciences of the United States of America*, *94*, 9905–9908. [PubMed] [Article]
- Atkinson, J., Campbell, F. W., Fiorentini, A., & Maffei, L. (1973). The dependence of monocular rivalry on spatial frequency. *Perception*, *2*, 127–133.
- Baumann, R., van der Zwan, & Peterhans, E. (1997). Figure–ground segregation at contours: A neural mechanism in the visual cortex of the alert monkey. *European Journal of Neuroscience*, *9*, 1290–1303. [PubMed]
- Blake, R., & Logothetis, N. K. (2002). Visual competition. *Nature Reviews: Neuroscience*, *3*, 13–21. [PubMed]
- Blake, R., O’Shea, R. P., & Mueller, T. J. (1992). Spatial zones of binocular rivalry in central and peripheral vision. *Vision Neuroscience*, *8*, 469–478. [PubMed]
- Bonneh, Y. S., Cooperman, A., & Sagi, D. (2001). Motion-induced blindness in normal observers. *Nature*, *411*, 798–801. [PubMed]
- Boutet, I., & Chaudhuri, A. (2001). Multistability of overlapped face stimuli is dependent upon orientation. *Perception*, *30*, 743–753. [PubMed]
- Bradley, A., & Schor, C. (1988). The role of eye movements and masking in monocular rivalry. *Vision Research*, *28*, 1129–1137. [PubMed]
- Breese, B. B. (1899). On inhibition. *Psychological Monographs*, *3*, 1–65.
- Breitmeyer, B. G., & Rudd, M. E. (1981). A single-transient masking paradigm. *Perception & Psychophysics*, *30*, 604–606. [PubMed]
- Campbell, F. W., Gilinsky, A. S., Howell, E. R., Riggs, L. A., & Atkinson, J. (1973). The dependence of monocular rivalry on orientation. *Perception*, *2*, 123–125.
- Campbell, F. W., & Howell, E. R. (1972). Monocular alternation: A method for the investigation of pattern vision. *Journal of Physiology*, *225*, 19P–21P. [PubMed]
- Carandini, M., Barlow, H. B., O’Keefe, L. P., Poirson, A. B., & Movshon, J. A. (1997). Adaptation to contingencies in macaque primary visual cortex. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *352*, 1149–1154. [PubMed]
- Carlson, T. A., & He, S. (2004). Competing global representations fail to initiate binocular rivalry. *Neuron*, *43*, 907–914. [PubMed]
- Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience*, *7*, 308–313. [PubMed]
- Crassini, B., & Broerse, J. (1982). Monocular rivalry occurs without eye movements. *Vision Research*, *22*, 203–204. [PubMed]
- Crovitz, H. F., & Lockhead, G. R. (1967). Possible monocular predictors of binocular rivalry of contours. *Perception & Psychophysics*, *2*, 83–85.
- Fukuda, H., & Blake, R. (1992). Spatial interactions in binocular rivalry. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 362–370 [PubMed]
- Furchner, C. S., & Ginsburg, A. P. (1978). “Monocular rivalry” of a complex waveform. *Vision Research*, *18*, 1641–1648. [PubMed]
- Georgeson, M. A. (1984). Eye movements, afterimages and monocular rivalry. *Vision Research*, *24*, 1311–1319. [PubMed]
- Georgeson, M. A., & Phillips, R. (1980). Angular selectivity of monocular rivalry: Experiment and computer simulation. *Vision Research*, *20*, 1007–1013. [PubMed]
- Graf, E. W., Adams, W. J., & Lages, M. (2002). Modulating motion-induced blindness with depth ordering and surface completion. *Vision Research*, *42*, 2731–2735. [PubMed]
- Heider, B., Meskenaitė, V., & Peterhans, E. (2000). Anatomy and physiology of a neural mechanism defining depth order and contrast polarity at illusory contours. *European Journal of Neuroscience*, *12*, 4117–4130. [PubMed]
- Kanai, R., & Kamitani, Y. (2003). Time-locked perceptual fading induced by visual transients. *Journal of Cognitive Neuroscience*, *15*, 664–672. [PubMed]
- Kaufman, L. (1963). On the spread of suppression and binocular rivalry. *Vision Research*, *3*, 401–415. [PubMed]
- Kitterle, F. L., & Thomas, J. (1980). The effects of spatial frequency, orientation, and color upon binocular rivalry and monocular pattern alternation. *Bulletin of the Psychonomic Society*, *16*, 405–407.
- Kleinschmidt, A., Büchel, C., Zeki, S., & Frackowiak, R. D. J. (2001). Human brain activity during spontaneously reversing perception of ambiguous figures. *Proceedings of the Royal Society of London. B, Biological Sciences*, *265*, 2427–2433. [PubMed]
- Lamme, V. A. (1995). The neurophysiology of figure–ground segregation in primary visual cortex. *Journal of Neuroscience*, *15*, 1605–1615. [PubMed]
- Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: Changing views in perception. *Trends in Cognitive Science*, *3*, 254–264. [PubMed]
- Leopold, D. A., Maier, A., Wilke, M., & Logothetis, N. K. (2004). Binocular rivalry and the illusion of

- monocular vision. In D. Alais & R. Blake (Eds.), *Binocular rivalry and perceptual ambiguity* (pp. 231–265). Cambridge, MA: MIT Press.
- Li, Z. (2002). A saliency map in primary visual cortex. *Trends in Cognitive Science*, 6, 9–16. [[PubMed](#)]
- Logothetis, N. K., & Sheinberg, D. L. (1996). Visual object recognition. *Annual Review of Neuroscience*, 19, 577–621. [[PubMed](#)]
- Lumer, E. D., Friston, K. J., & Rees, G. (1998). Neural correlates of perceptual rivalry in the human brain. *Science*, 280, 1930–1934. [[PubMed](#)]
- Mapperson, B., Bowling, A., & Lovegrove, W. (1982). Problems for an after-image explanation of monocular rivalry. *Vision Research*, 22, 1233–1234. [[PubMed](#)]
- Mapperson, B., & Lovegrove, W. (1984). The dependence of monocular rivalry on spatial frequency: Some interaction variables. *Perception*, 13, 141–151. [[PubMed](#)]
- Mitchell, J. F., Stoner, G. R., & Reynolds, J. H. (2004). Object-based attention determines dominance in binocular rivalry. *Nature*, 429, 410–413. [[PubMed](#)]
- Nakayama, K., Shimojo, S., & Silverman, G. H. (1989). Stereoscopic depth: Its relation to image segmentation, grouping, and the recognition of occluded objects. *Perception*, 18, 55–68. [[PubMed](#)]
- O'Regan, J. K., & Noe, A. (2001). A sensorimotor account of vision and visual consciousness. *Behavioral and Brain Sciences*, 24, 939–973. [[PubMed](#)]
- O'Shea, R. P. (1998). Effects of orientation and spatial frequency on monocular and binocular rivalry. In N. Kasabov, R. Kozma, K. Ko, R. O'Shea, G. Coghill, & T. Gedeon (Eds.), *Proceedings of the Fourth International Conference on Neural Information Processing (ICONIP '97)* (pp. 67–70). Singapore: Springer-Verlag.
- O'Shea, R. P., Sims, A. J., & Govan, D. G. (1997). The effect of spatial frequency and field size on the spread of exclusive visibility in binocular rivalry. *Vision Research*, 37, 175–183. [[PubMed](#)]
- Paffen, C. L. E., te Pas, S. F., Kanai, R., van der Smagt, & Verstraten, F. A. J. (2004). Center-surround interactions in visual motion processing during binocular rivalry. *Vision Research*, 44, 1635–1639. [[PubMed](#)]
- Pritchard, R. M. (1958). Visual illusions viewed as stabilized retinal images. *Quarterly Journal of Experimental Psychology*, 10, 77–81.
- Rauschecker, J. P., Campbell, F. W., & Atkinson, J. (1973). Colour-opponent neurons in the human visual system. *Nature*, 245, 42–43. [[PubMed](#)]
- Riani, M., Tuccio, M. T., Borsellino, A., Radilova, J., & Radil, T. (1986). Perceptual ambiguity and stability of reversible figures. *Perceptual and Motor Skills*, 63, 191–205. [[PubMed](#)]
- Rossi, A. F., & Paradiso, M. A. (1995). Feature-specific effects of selective visual attention. *Vision Research*, 35, 621–634 [[PubMed](#)]
- Sanchez-Vives, M. V., Nowak, L. G., & McCormick, D. A. (2000). Cellular mechanisms of long-lasting adaptation in visual cortical neurons in vitro. *Journal of Neuroscience*, 20, 4286–4299. [[PubMed](#)] [[Article](#)]
- Shimojo, S., Kamitani, Y., & Nishida, S. (2001). After-image of perceptually filled-in surface. *Science*, 293, 1677–1680. [[PubMed](#)]
- Sindermann, F., & Luddeke, H. (1972). Monocular analogues to binocular contour rivalry. *Vision Research*, 12, 763–772. [[PubMed](#)]
- Suzuki, S., & Grabowecky, M. (2002). Overlapping features can be parsed on the basis of rapid temporal cues that produce stable emergent percepts. *Vision Research*, 42, 2669–2692. [[PubMed](#)]
- Tehovnik, E. J., Slocum, W. M., & Schiller, P. H. (2003). Saccadic eye movements evoked by microstimulation of striate cortex. *European Journal of Neuroscience*, 17, 870–878. [[PubMed](#)]
- Troxler, D. (1804). Ueber das Verschwinden gegebener Gegenstaende innerhalb unseres Gesichtskreises. In K. Himly & J. A. Schmidt (Eds.), *Ophthalmologische Bibliothek II* (pp. 1–53). Jena, Germany: Frommann.
- Wade, N. J. (1975). Monocular and binocular rivalry between contours. *Perception*, 4, 85–95. [[PubMed](#)]
- Wilke, M., Logothetis, N. K., & Leopold, D. A. (2003). Generalized flash suppression of salient visual targets. *Neuron*, 39, 1043–1052. [[PubMed](#)]
- Wilson, H. R., Krupa, B., & Wilkinson, F. (2000). Dynamics of perceptual oscillations in form vision. *Nature Neuroscience*, 3, 170–176. [[PubMed](#)]
- Wolfe, J. M. (1984). Reversing ocular dominance and suppression in a single flash. *Vision Research*, 24, 471–478. [[PubMed](#)]
- Wong, E., & Weisstein, N. (1982). A new perceptual context-superiority effect: Line segments are more visible against a figure than against a ground. *Science*, 218, 587–589. [[PubMed](#)]
- Wong, E., & Weisstein, N. (1983). Sharp targets are detected better against a figure, and blurred targets are detected better against a background. *Journal of Experimental Psychology: Human Perception and Performance*, 9, 194–201. [[PubMed](#)]