Suppression wave dynamics: visual field anisotropies and inducer strength.

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Abstract

We used binocular rivalry and generalized flash suppression to identify several new shared properties of traveling suppression waves. A strong relationship was found between suppression wave speed and induction pulse strength: increasing the contrast or dot density of the induction pulse led to an increase in wave speed. Evidence of visual field anisotropies in wave propagation speeds were also seen, with suppression waves decelerating as they travel towards the fovea. This deceleration could not be accounted for by cortical magnification in lower level brain areas, suggesting an important role for other, yet to be identified, factors.

1. General introduction

As any good magician or pickpocket will attest, people are often unaware of many of the objects and events that surround them. Experimentally, it has been shown that even when attention is focused intently on an object, that object can be rendered perceptual invisible with a few simple stimulus manipulations. One such method used to suppress stimuli from conscious awareness is binocular rivalry (BR) (Wheatstone, 1838; Levelt, 1965; Blake & Logothetis, 2002). Binocular rivalry arises when one eye receives a significantly different image than the other eye. These incompatible images compete for perceptual dominance, causing them to perceptually alternate. Many studies have used BR to investigate the neural mechanisms underlying conscious experience. However, until recently, little was known about the complementary process of conscious suppression. Here we are interested in the mechanisms by which perceptually salient stimuli come to be suppressed, with the specific aim of identifying the dynamic properties of perceptual suppression.

Although the mechanisms underlying suppression are still poorly understood, it is clear from observation that the transition from suppression to dominance is often gradual and appears to propagate in a wavelike fashion. A recent study showed that it is possible to control the starting point of this transition by generating a brief contrast increment (pulse) at one location of the suppressed image. At the point of the pulse, the previously suppressed image will generally break through and its dominance will spread and travel in a wavelike manner (Wilson, Blake, & Lee, 2001; Lee, Blake, & Heeger, 2005). This technique has opened up the possibility of systematically studying suppression propagation. However, there is one important limitation with BR: suppression of one target image is necessarily accompanied by dominance of the alternate image in the corresponding region of visual space. This makes it impossible to measure the spread of suppression independent of dominance and, more importantly, to dissociate the relative interacting contributions of the suppressed and dominant visual input.

Wilke, Logothetis, and Leopold (2003, 2006) developed a paradigm, called generalized flash suppression (GFS), which overcomes this problem by generating perceptual suppression in an area spatially adjacent to the suppression inducing stimulus. In order to induce disappearance of targets, GFS combines the dichoptic viewing of binocular rivalry flash suppression (BRFS: Wolfe, 1984) and large monoptic motion

fields typical of motion induced blindness (MIB: Bonneh, Cooperman, & Sagi, 2001). In GFS, a target stimulus is presented to one eye. After several hundred milliseconds, a mask pattern consisting of small moving dots is suddenly presented to both eyes. Even though the mask pattern does not overlap the spatial location of the targets, they are perceived to disappear for periods of seconds (Wilke et al., 2003). The fact that the latency of the perceptual suppression in GFS increases with the target's distance from the mask pattern suggests that suppression propagates successively through adjacent areas of the visual field.

Despite these differences, the obvious parallels between the suppression seen in BR and GFS lead Wilke et al. (2003) to suggest that suppression in GFS may propagate in a wave-like manner similar to that in BR (Wilson et al., 2001; Lee et al., 2005). While the labeling of these suppression effects as wave-like is convenient and allows for an intuitive description of the perceptual experience, the primary characteristics of and the degree to which these are shared between suppression phenomena remain unknown. As researchers continue to investigate how the brain generates perceptual suppression, one critical question is whether there are multiple mechanisms or only one. By carefully manipulating properties in both BR and GFS, the present study attempts to: 1) identify the factors responsible for the spatio-temporal pattern of suppression; 2) determine whether these factors are common for GFS and BR.

2. Experiment 1

Previous studies show that it is possible to create a suppression wave with a constant speed. A psychophysical study using BR (Wilson et al., 2001) measured cortical brainwave speeds of 2.24 cm/s and an fMRI study (Lee et al., 2005) reported similar speeds between 1.6 and 2.0 cm/s. Despite the consistency of the speeds measured, it was also noted that the inducer does not always trigger a wave at the time or location of the pulse. It is not clear from these studies which features of the inducer influence either the probability that a wave is initiated, or the speed of its subsequent propagation. As it is known that increasing stimulus contrast increases the alternation rate during binocular rivalry (Levelt, 1965), it is possible that this increased alternation rate reflects an increased likelihood of suppression wave initiation or propagation rate. Here we investigate the effect of changing the contrast of the induction pulse on the initiation probability and dynamics of traveling suppression waves during BR.
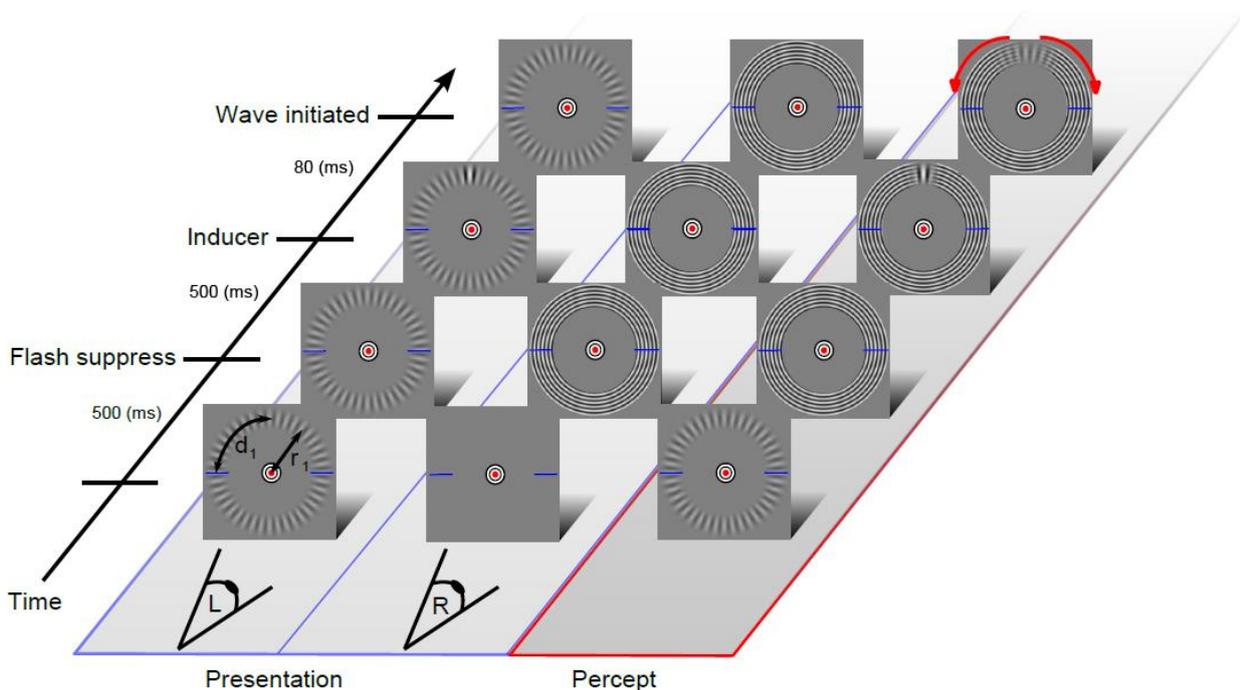
Figure 1. Experiment 1 stimulus consisted of two annuli with a 3.0° radius (r_1) and a 1° width with a gaussian contrast adjustment. One annulus with radial gratings was presented to one eye followed by the second annulus containing concentric gratings presented to the other eye. This procedure resulted in a dominant percept of the newly introduced concentric grating. A brief inducer pulse (60% or 90% contrast increment) was then presented at the top of the radial annulus gradually returning dominance to the radial grating which is perceived to spread out over the concentric gratings (d_1 – 4.7 deg) in a wave-like manner from the inducer location (shown in the right column). The subject's task was to report when the dominance of the radial grating had reached either of the horizontal blue lines transecting the annulus (the distance from the inducer to each blue line was 4.7°).

2.1 Methods

2.1.1 Participants

Two authors (MN & OC) and three naïve observers took part in this experiment. All participants had normal or corrected to normal vision and were experienced psychophysical observers recruited from the Vision Sciences lab at Harvard University. The experiments were approved by the Harvard University Committee on the Use of Human Subjects in Research, and conformed to the standards of the Declaration of Helsinki.

2.1.2 Stimuli

Stimuli were generated in MATLAB 7.1 using Psychtoolbox (Brainard, 1997; Pelli, 1997) and presented on a 17" monitor (60Hz, 1024x786 pixels) with a grey background. The stimuli used in the experiment were based on those used by Wilson et al. (2001) and Lee et al. (2005). Stimuli consisted of either high contrast concentric, or low contrast radial, sinewave gratings presented in an annulus around fixation (Fig. 1). Background and mean stimulus luminance was 22 cd/m^2. The radial grating had a 30% Michelson contrast, a spatial frequency of ~6.5 cycles/deg. The concentric grating had a 70% Michelson contrast, a spatial frequency of ~0.5 cycles/deg. Each annulus had an inner and outer radius of 2.5° and 3.5° respectively with the edges of the annulus smoothed using a Gaussian function. Two 0.05° x 1.0° blue lines transecting the annulus along the left and right horizontal meridian were presented dichoptically. The inducer was a 0.4° x 1° contrast increment to either a 60% or 90% Michelson contrast presented in the upper-most (12 o'clock) region of the low contrast radial annulus. The distance around the annulus from the inducer to either of the blue markers was approximately 4.7°.

2.1.3 Procedure

Observers viewed the stimuli through a mirror-stereoscope and were asked to maintain fixation on a central red dot, while head position was stabilized using a chin rest that assured a steady screen distance of 40cm. Participants were first presented with the low contrast radial grating to one eye. After 500ms a similar size high contrast concentric annulus was presented in the corresponding retinal location of the other eye

(BRFS – Wolfe, 1984) which generally resulted in perceptual suppression of the low contrast radial annulus and dominance of the concentric annulus. An additional 500ms later, the inducer was flashed for 80ms, causing the previously suppressed image to become perceptually dominant in a wave propagating away from the induction point. The observer was instructed to press a button when the wave reached either one of the transecting blue marks. The button response caused the trial to end.

Next, the observer was asked whether a complete wave-like event was experienced from the location of the inducer to the blue test line. The trial was repeated if participants failed to respond within 2s or if they reported that the wave was either incomplete or irregular. Observers initiated the next trial by pressing the space bar. The experiments consisted of two blocks of 100 successful trials (approximately 15min each) and the two contrast conditions were randomly presented throughout each block. Paired t-tests were performed on the mean traveling wave latency and initiation probability.

As reaction times lengthen the measured suppression wave latencies, we ran a control experiment in which observers were instructed to press a button as soon as they detected the onset of the inducer pulse. The mean RT measured in the control experiment was subtracted, per observer, from the mean traveling wave latency in each condition. Reaction times (RTs) outside the range of 3 standard deviations from the mean were discarded.

2.2 Results & discussion

The mean travel latency (travel latencies were normally distributed for 4 out of 5 observers) was 512ms in the low contrast condition (SD: 244ms) and 466ms in the high contrast condition (SD: 241ms) (Fig. 2). The mean difference between the disappearance latencies for the low and high contrast pulse was a significant 46ms (SD: 20ms) [$t(4)=5.2382$, $p<0.01$] which corresponds, depending on the observer, to an increase of speed between 8-32% with a high contrast induction pulse as compared to a low contrast pulse. Note the large differences between observers in wave speeds (5.9-18.0 deg/s), but that all subjects showed the same effect of decreasing wave speed with the low contrast inducer (Fig. 2A) The likelihood that an appropriate wave was initiated (incomplete or irregular waves were not included in the initiation probability) was also much lower in the low contrast pulse condition than in the high contrast pulse condition for all subjects (Fig. 2B). The

mean initiation probability was 92.46% for a high contrast inducer (SD: 4.90) and significantly lower for the

low contrast inducer at 83.15% (SD: 10.88) (t(4)=3.3663, p<0.05).

Our results are the first to illustrate this tight link between the traveling suppression wave inducer and

the following wave speed. As it has recently been shown that motion in the suppressed eye's stimulus can

speed up the traveling wave (Knapen, van Ee, & Blake, 2007), we were curious whether wave speeds could

be modified by other factors, once the wave had begun propagating across visual space.
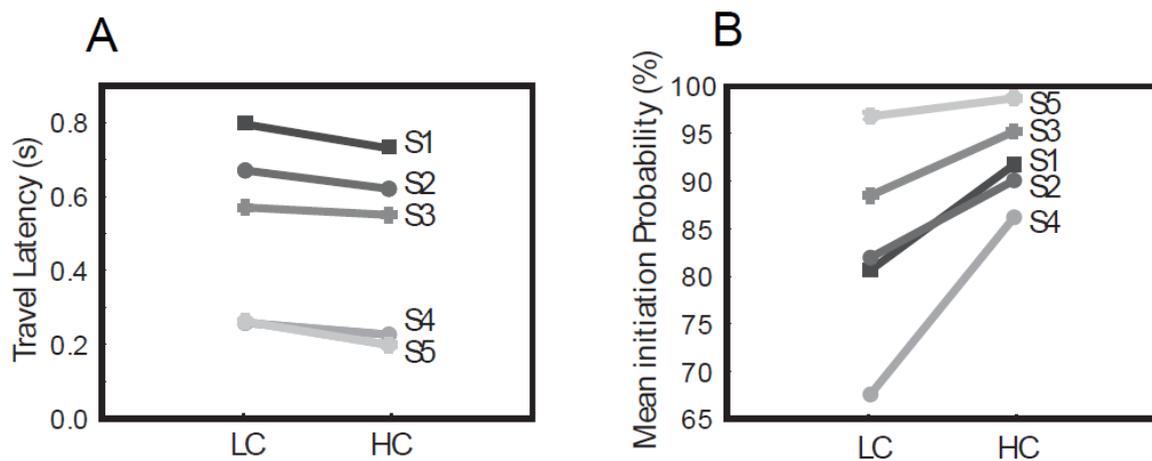
Figure 2. The effect of inducer strength on traveling wave propagation. Low contrast (LC) and high contrast (HC) pulses are shown on the x-axis respectively. (A) Mean travel latencies and (B) initiation probability of the traveling waves for each observer. Both travel speed and initiation probability of a wave is respectively faster and greater in the high contrast inducer condition for all participants.
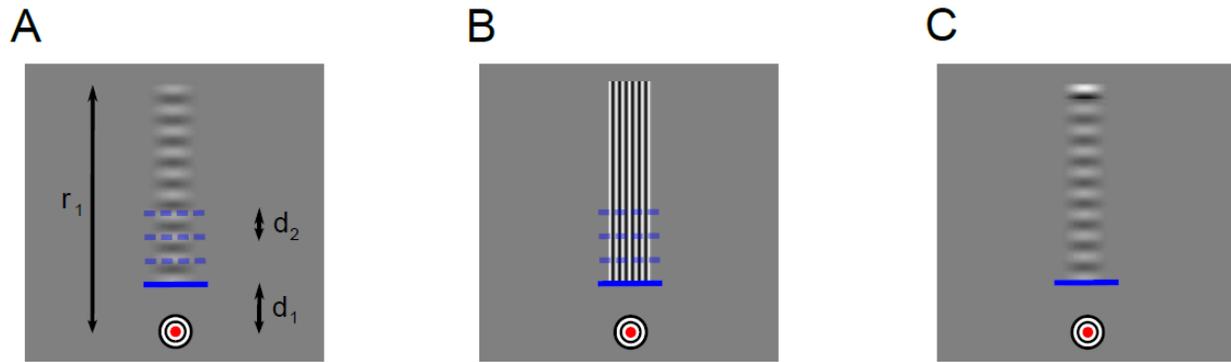
3. Experiment 2

Experiment 1 showed that the induction probability and subsequent speed of suppression waves is not fixed but depends on the strength of the inducer (i.e. the contrast). This raises the question of whether suppression propagation shows similar variability across different areas of the visual field. An earlier study fixed the eccentricity of the wave's path and found that it had a constant speed (Wilson et al., 2001). To test whether the speed remains constant at different eccentricities, we measured the propagation of traveling waves towards the fovea.

3.1 Methods

MN, OC and two naive observers participated in experiment 2. To create a traveling wave in BR that propagates towards the fovea, we used a rectangle extending from the periphery to the fovea (Fig. 3). The inducer had a fixed contrast (90%) and was presented as a brief pulse at the outer-most point of the rectangle 6° from fixation. Wave latency was measured at four different eccentricities (1.2, 1.6, 2.0, & 2.4° of visual angle from the fixation point). All other aspects of the apparatus and procedure used were identical to that described above in experiment 1.

As wave latencies were measured at different distances from fixation, it is possible that any observed differences in response times may reflect a difference in speed at which people are able to detect and report the arrival of the wave at different locations in the visual field. To make certain that wave latencies were not influenced by the effects of spatial anisotropies on response latencies, we ran a control experiment with four new naïve observers in which waves were simulated at a fixed speed that was randomly chosen per trial from a 15-30 deg/s range (all other aspects of the apparatus, stimuli and procedure were identical to that described for the main experiment 2). Median values were analyzed using a repeated measures ANOVA to compare the travel latencies per eccentricity condition. Trend tests were performed to analyze the development of the median travel latencies as a function of eccentricity.

Figure 3. Experiment 2 stimuli. A) A low contrast horizontal sinewave grating was first presented to one eye and this was followed by B) a high contrast vertical grating presented to the other eye. C) After a period of time an inducer pulse was presented, triggering a suppression wave that travels from top at an eccentricity of 6.0° (r_1), to bottom at an eccentricity of 1.2 (d_1). To find out whether the wave has a constant speed as it travels towards the fovea, the travel latency was measured at four different locations; each separated by a 0.4° (d_2) difference in eccentricity (indicated by the dashed lines in A and B). Only one eccentricity was tested in each trial.

3.2 Results & discussion

Figure 4A shows the latency of the suppression wave as a function of eccentricity for all observers. There was a significant increase in median latency values 656ms, 659ms, 669ms and 699ms at eccentricities closer to the fovea away from the inducer ($F(3)=9.554$, $p=0.004$). For three of the four observers, this increase in latency towards the fovea appeared to be quadratic (data not shown). Indeed, trend analysis over all observers showed that a cubic fit achieves a higher significance level ($F(1)=29.061$, $p=0.013$) compared to a linear fit of the same data ($F(1)=12.533$, $p=0.034$). Propagation speeds between the four distances (1.2, 1.6, 2.0, & 2.4 and distal from the fixation point) are estimated at 13.4 deg/s, 39.5 deg/s and 157.0 deg/s respectively (Fig 4B), and indicate a clear deceleration of suppression waves. As activity in visual brain area V1 is found to spatiotemporally reflect traveling suppression waves (Lee, Blake, & Heeger, 2007), it is a plausible neural locus for the initiation and processing of suppression waves. Because central visual regions are overrepresented in areas such as V1 (also known as the cortical magnification factor, Daniel and Whitteridge, 1961), the observed deceleration could be absent in V1 activity patterns when asymmetric cortical distances are taken into account. In other words, if the spread of activity in V1, caused by traveling suppression waves, progresses with a constant velocity towards the relatively larger brain regions that process the central field of vision, the cortical magnification factor could explain the perceptual experience of deceleration. Using

cortical magnification values from Larsson & Heeger (2006) we calculated the predicted speed across the three eccentricity differences based on a constant cortical speed of 16.62cm/s. At this cortical speed the corresponding differences in degrees of visual angle would only be 13.4 deg/s, 17.19 deg/s & 19.86 deg/s. The minimal deceleration found in these values indicates that the difference in speed cannot be accounted for by cortical magnification in V1. Also in contrast to the retinal speeds, the simulated wave latencies showed a significant linear increase ($F(3)=29.411$, $p<0.001$; linear trend: $F(1)=85.346$, $p<0.001$) (Fig 4A). The calculated propagation speeds for the simulated waves were 38.69 deg/s, 23.47 deg/s, and 30.62 deg/s (Fig 4B). The fact that these propagation speeds were relatively consistent across eccentricities indicates that changes in speed reported for the illusory suppression waves, are unlikely to be due to response error. In summary, the results of experiment 1 and 2 show two new characteristics that influence the speed of traveling suppression waves: the strength of its inducer; and its location in the visual field. The following two experiments focus on the generality of these characteristics by measuring suppression effects induced by a different experimental paradigm, namely GFS.
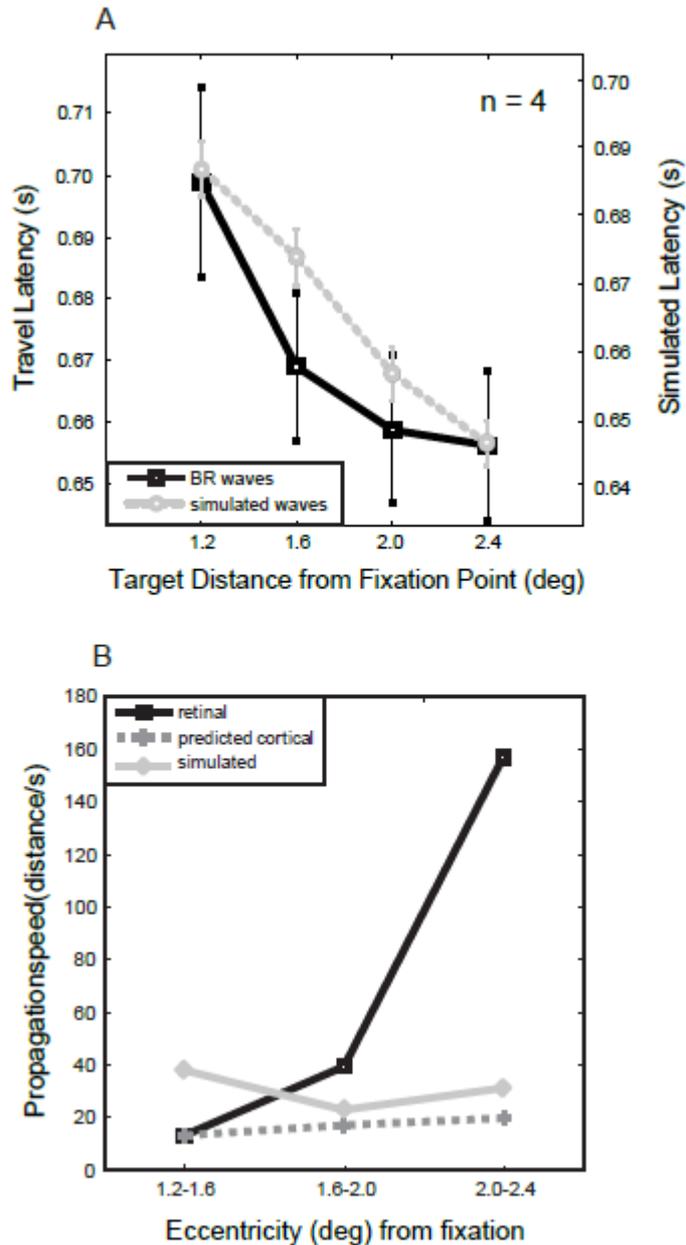
Figure 4. (A) Median traveling wave speed (s) with standard errors, as a function of eccentricity for the real (left y-axis) and simulated control (right y-axis) experiments. The linear function of the simulated waves shows that reaction times did not account for the deceleration of waves found in the BR wave experiment. (B) The median traveling wave propagation speeds (s) based on travel latency as a function of eccentricity (deg of visual angle in respect to the retinal image) presented in solid black. The propagation speed increases as a function of eccentricity which indicates that a wave slows down as it travels towards the fovea. The speeds were calculated between the target locations that match the locations used in experiment 2. The dashed light grey line illustrates the change in wave speed predicted on the basis of cortical magnification alone (with a constant speed of 16.62cm/s). The solid light grey line presents the calculated speeds of the simulated waves in the control experiment.

4. Experiment 3

As mentioned in the introduction, the BR paradigm makes it impossible to measure the spread of suppression independent of the corresponding spread of perceptual dominance. In contrast, the GFS paradigm allows us to investigate the spread of suppression independent of any changes in perceptual dominance. Wilke et al. (2003) argued that suppression waves could underlie their GFS results. It is unclear, however, whether these suppression waves are identical to those seen in BR, or whether they are simply wave-like. In experiment 3 we looked at whether the wave characteristics found in BR are the same in GFS. Wilke et al. (2003) previously reported that GFS waves traveled at a cortical speed of 0.5cm/s, which is slower than the slowest speed calculated for BR in our experiments as well as those reported previously in other studies (Wilson et al., 2001). Here, we were interested to see whether these apparent differences in travel speeds can be explained by properties of the inducing stimuli.
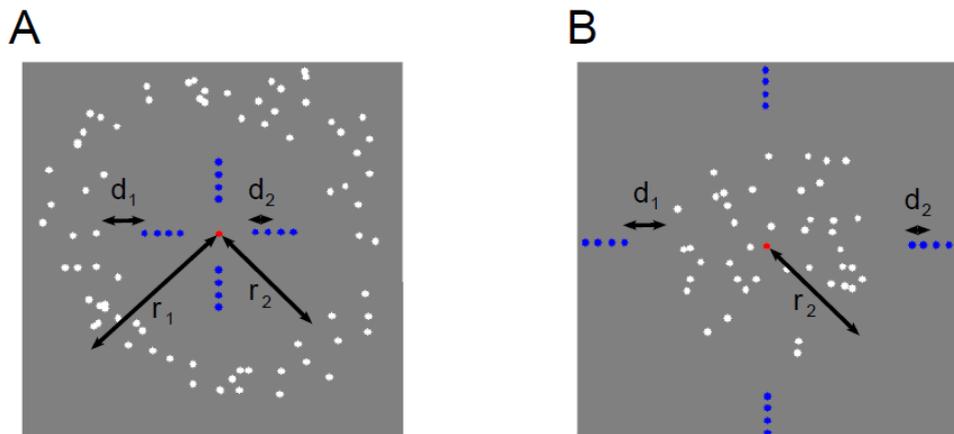
Figure 5. (A) The targets were presented at one of four eccentricities from fixation and the distances between targets (d_2) were the same as in experiment 2. The induction stimulus was presented in a surrounding annulus 3.6 (r_2) to 6.3 (r_1) degrees from fixation. (B) In experiment 4, the opposite configuration was used with the induction stimulus presented centrally between 0 and 3.6 (r_2) degrees from fixation. The targets were presented at one of 4 eccentricities extending towards the periphery and the minimum distance between the targets and the induction stimulus was 1.2 degree (d_1). In all cases, 4 targets were presented at the specified eccentricity (1 target along each of the 4 cardinal axis).

In previously reported studies, the inducer in GFS consisted of randomly moving dots with a certain density. Since it is known that increasing the density of the inducer results in an increase of the suppression effect (Wilke et al, 2003), it is an appealing thought that the "strength" of the inducer influences the suppression

strength and the speed of the wave. If GFS suppression waves are similar to waves in BR, inducer strength should influence their speed and initiation probability and perhaps their duration of disappearance as well.

4.1 Methods

Authors MN, OC, and three naive observers took part in experiment 3. In the first condition, four blue target dots were presented centrally along the vertical and horizontal axis at either 1.2, 1.6, 2.0, or 2.4° eccentricity. These eccentricities corresponded to four different distances (2.4, 2.0, 1.6, & 1.2°) distal from the inducer flash. The GFS inducer consisted of randomly moving dots (speed=3.00°/s, maximum angle of deviation = 45 °/frame) presented in a surrounding annulus that extended between a radius of 3.6° and 6.3° from fixation (Fig. 5A). Dots going out of bounds were relocated at the opposing boundary at the same visual angle. Targets and moving dots each had a diameter of 0.27°.

Three different suppressor dot densities (0.25, 0.50, or 1.00 dots/deg^2) and the four target distances were randomly varied between trials (12 conditions). Targets were viewed monocularly and after 1s a stimulus (inducer/suppressor) was flashed to both eyes dioptically. If one or more targets disappeared after the presentation of the inducer, observers were asked to immediately indicate this initial disappearance of any target by pressing a button. The button was then released as soon as this same target reappeared. The trial ended when observers reported the reappearance of the targets. If no disappearance was reported for 8s the trial was automatically terminated. The experiment consisted of 288 trials divided in two blocks of 144 trials and each block contained 12 trials of all 12 conditions, presented in a random order. The apparatus and all other aspects of the methodology were identical to that described in the preceding experiments.

Median values were analyzed using a repeated measures ANOVA to compare the disappearance latencies and disappearance durations across eccentricities and inducer strengths. Trend tests were performed to analyze how the median disappearance latencies and disappearance durations developed towards higher eccentricity.

4.2 Results & discussion

Figure 6 presents both median disappearance latencies (A) and median disappearance durations (B) as a function of inducer density and target location. There was a significant difference in disappearance latency as a function of distance towards the fovea ($F(3)=30.161$, $p<0.001$). A trend analysis confirmed that the increase of disappearance latency was quadratic ($F(1)=8.229$, $p<0.05$), indicating that the wave of suppression slows down systematically as it moves towards the fovea. From these results we estimated that our GFS inducing annulus caused retinal propagation speeds of 0.28, 0.35, and 1.70 deg/s and cortical speeds of 0.34, 0.34, 1.34cm/s between distances of 1.2, 1.6, 2.0, and 2.4 deg distal from the induction point respectively. The target distance also had a significant effect on disappearance duration, with closer targets disappearing for a greater time ($F(3)=5.982$, $p<0.01$). A trend analysis showed a linear decrease in disappearance duration, for target locations further from the inducer and closer towards the fovea ($F(1)=9.512$, $p<0.05$).

Increasing the dot densities of the surrounding inducer from 0.25 to 0.5 and 1.0 dots/deg, resulted in mean disappearance probabilities of 85.6% (SD: 14.2), 91.0% (SD: 8.6), and 92.1% (SD: 7.5) respectively. This relationship between disappearance probability and dot density showed a clear positive trend but differences in disappearance probabilities between the dot densities did not reach significance ($F(2)=2.302$, $p=0.162$). The density of the inducer also had an overall effect on disappearance latencies ($F(3)=2.715$, $p=0.126$) but not on the duration of disappearance ($F(3)=1.212$, $p=0.347$). Although the observed trend towards lower density flashes taking longer to produce a target disappearance than higher density flashes did not reach significance, the findings mirror significant effects previously reported (Wilke et al, 2003). The lack of significance in the current study likely reflects a ceiling effect. In the previous study (Wilke et al., 2003), density had an effect on disappearance probabilities in the range of 0-80% but not for probabilities between 80-100%.

These results show that like BR induced suppression waves, GFS suppression wave speed is not fixed during propagation, but slows down as the wave travels towards the fovea. In the following experiment we investigated whether this slowing down was specific to the foveal direction of the wave.
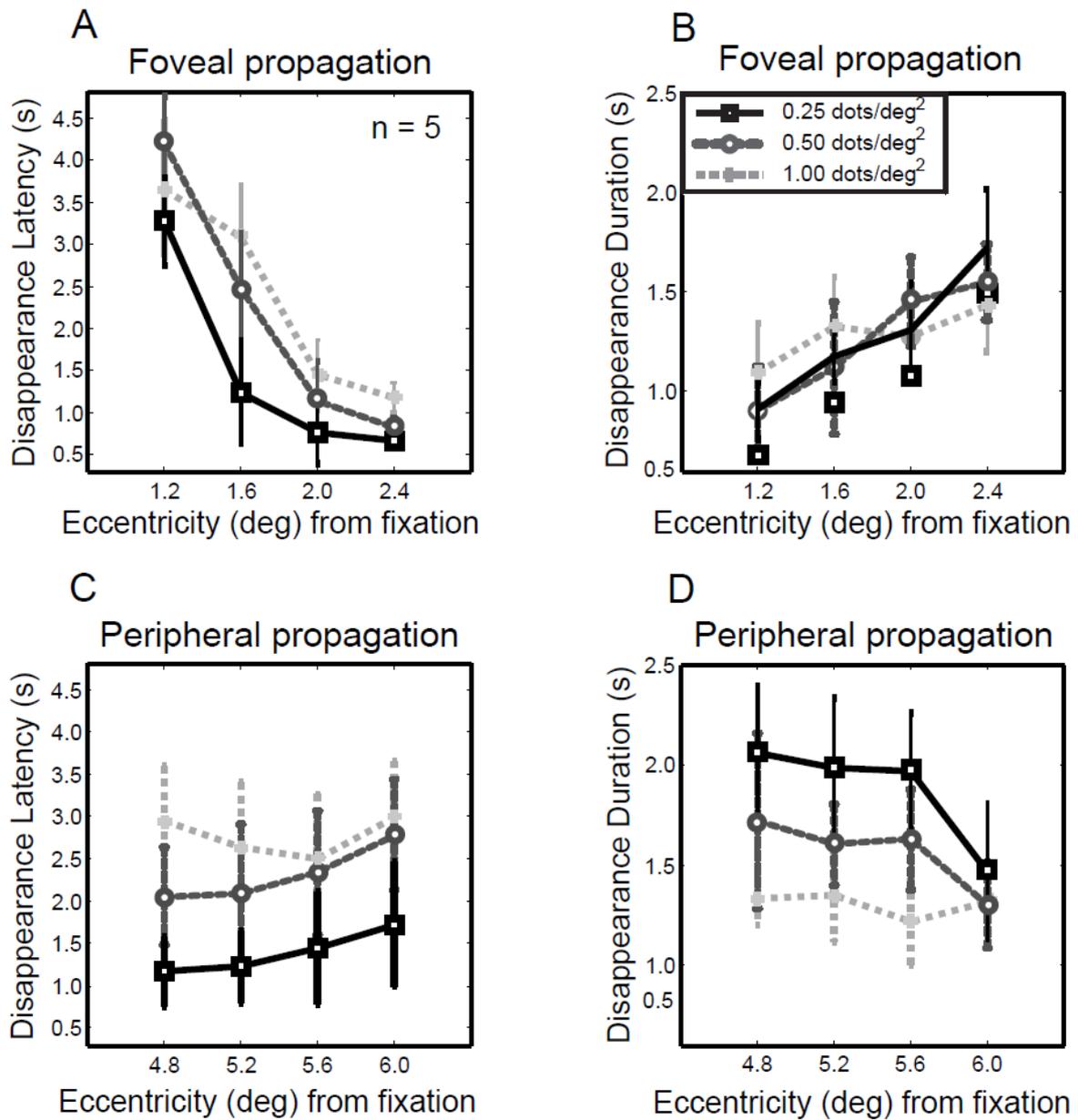
Figure 6. The disappearance latency (A and C) and duration (B and D) of the targets when the dot pattern is either flashed in an annulus around the targets (A and B) or centrally with the targets located in the periphery (C and D). Latencies quadratically decrease if waves travel toward the fovea (A) and inducer density seems to influence both disappearance latencies and durations (A, C, and D). Data points and error bars represent the medians and standard error of data pooled across all subjects.

5. Experiment 4

To investigate whether this deceleration was specific to propagation towards the fovea, or whether we had identified a more general principle for traveling waves, a fourth experiment measured the propagation of suppression waves away from the fovea, towards the peripheral visual field.

5.1 Methods

In this experiment the observers, stimuli, apparatus, and procedure were as described in experiment 3, the only difference being that the inducer was presented centrally, and the targets in the periphery (Fig. 5B). Target eccentricities were 4.8, 5.2, 5.6, or 6.0° and their relative distances from the inducer were the same as in experiment 3 (i.e. 1.2, 1.6, 2.0, & 2.4°).

5.2 Results & discussion

Changing the dot density of the central inducer from 0.25, 0.5 and 1.0 dots/deg had a systematic effect on the disappearance latencies (Fig. 6C), with lower density flashes taking significantly longer to produce a target disappearance than higher density flashes ($F(3)=7.251$, $p<0.05$; linear trend: $F(1)=8.247$, $p<0.05$). Inducer density also had a significant effect on the disappearance duration ($F(3)=7.440$, $p<0.05$) wherein higher densities produced longer disappearance durations (linear trend: $F(1)=12.083$, $p<0.05$) (Fig. 6D). Inducer density had no effect on disappearance probability ($F(2)=0.331$, $p=0.727$).

Target eccentricities had a minor but non-significant effect, leading to slightly increases in disappearance latencies (mean: $4.8° = 2.06s$; $5.2° = 1.98s$; $5.6° = 2.10s$; $6.0° = 2.50s$. $F(3)=2.816$, $p=0.084$), and decreases in disappearance duration respectively (mean: $4.8° = 1.70s$; $5.2° = 1.65s$; $5.6° = 1.60s$; $6.0°$ $1.36s$; $F(3)=1.497$, $p=0.265$).

These results suggest that increasing the strength of the central inducer results in both strengthening of the inhibitory effects of the waves and the speed of the propagation, but there is negligible slowing

between the ranges of peripheral eccentricities used in the current experiment. The deceleration of waves appears to be specific to foveal propagations.

As the target sizes in experiment 3 were held constant at different eccentricities, the parts of cortical area V1 responsible for processing the more foveally presented targets was larger than the cortical area that processed the peripherally located targets. Because the foveal targets received more visual processing, this cortical magnification effect might have biased the results making the foveal targets slower and less likely to disappear than the peripheral targets. The following experiment investigated this possibility.

6. Experiment 5

To assess whether differences between foveal and peripheral representation of the targets may have contributed to the reduction in propagation speeds calculated in experiment 3, we performed a final experiment in which the targets were kept constant and the inducer was presented at variable eccentricities.

6.1 Methods

MN and 4 naïve subjects participated in this experiment. Across the different trials, the target eccentricity was kept constant at 1.2° and inducer eccentricity (i.e. the inner boundary of the annulus) was randomly varied between 2.0 and 4.0°. In order to ensure that the inducer was stimulating a similar sized area of visual cortex, the width of the inducer's annulus was adjusted such that it equated to approximately 8mm of primary visual cortex. In all other respects the stimuli, apparatus, and procedure were identical to that used in experiment 3 and 4. Trials were ended as soon as subjects reported target disappearance by pressing a button. Median values were analyzed using a repeated measures ANOVA to compare the disappearance latencies per eccentricity condition. An additional analysis was performed to test for a trend of disappearance latencies across eccentricities.

6.2 Results & discussion

Differences in target disappearance latencies between foveal inducers were larger than between peripheral inducers (Fig. 7). The nonlinear development of the latency function indicates a decrease of speed when suppression waves travel towards the fovea ($F(7)=24.518$, $p<0.001$; quadratic trend: $F(1)=5.171$, $p<0.05$). Because the deceleration is present in the data while we controlled for the size of the cortical area that processes the target and mask, it seems unlikely that cortical magnification effects are responsible for the speed values found in experiment 3. Together with the results of experiment 2, this adds further evidence that suppression waves slow down as they travel towards foveal regions of visual space.
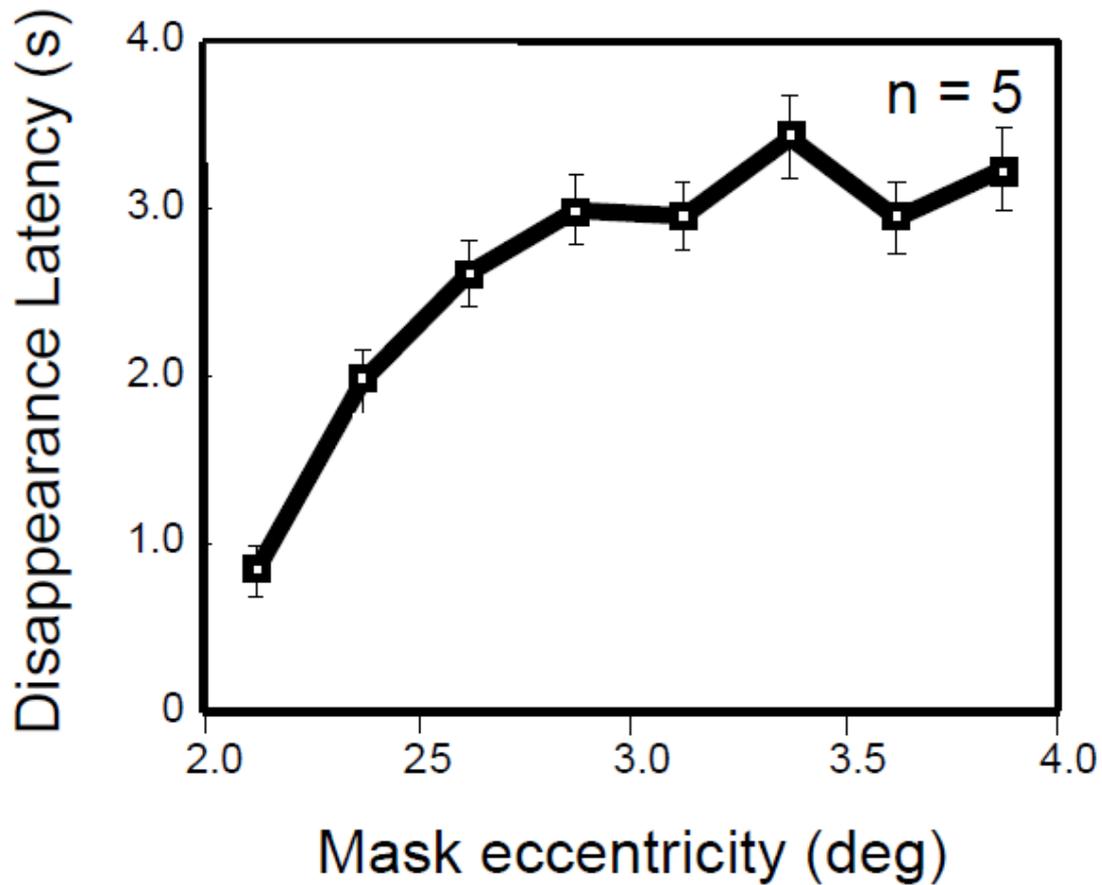
Figure 7. Target disappearance latencies (s) as a function of mask eccentricity (deg) for all 5 subjects. Medians and standard errors were calculated by dividing pooled data into 8 bins. The nonlinear increase of the function indicates the deceleration of waves when traveling towards the fovea. As target eccentricity was kept constant and the annulus width was adjusted to the cortical magnification, these results exclude the possibility that stimulus sizes underlie the very similar results found in experiment 3.

7. General discussion

In conclusion, we report a number of new characteristics of suppression wave propagation. Firstly, we have demonstrated that the latency and duration of perceptual suppression is systematically influenced by the "strength" of the inducer. Secondly, the suppression wave decelerates as it travels towards the fovea. Thirdly, as these effects were seen in both BR and GFS, it is tempting to suggest that the two phenomena may share a common neural origin. The most surprising result of this study, though, was the finding that the deceleration could not be accounted for by cortical magnification alone.

Our findings fit within a new body of research suggesting that perceptual suppression is propagated in a wave-like fashion throughout the cortex. Studies that used voltage sensitive dye imaging to image waves evoked by electrical pulses in brain slices of animals, found wave propagation speeds in the range between 1-5 cm/s, values that are very close to the speed values found in this study (Bai, Huang, Yang, & Win, 2006; Sanchez-Vives & McCormick, 2000). In support of the proposed existence of traveling suppression waves underlying GFS, recent electrophysiological recordings from awake monkeys found that the latency of V1 cell responses to a surround onset increased systematically as the distance between surround and receptive field border increased (M. Wilke, personal communication). Evidence of similar wave-like effects in V1 was seen in a recent human fMRI study that found activity in V1 to be correlated with the observation of a traveling wave in binocular rivalry (Lee et al., 2007). While the current GFS propagation speeds are similar to those found by Wilke et al. (2001), it is noteworthy that our calculated BR speed values are approximately 10 fold faster than the 1.6–2.24cm/s reported in earlier studies (Wilson et al., 2001). Although the general pattern of slowing was seen consistently across observers, it is difficult to know how much significance to place on the difference in speeds calculated between BR and GFS when taking the stimulus-related differences into account. Beyond the potential differences in wave speed, it is also possible that small errors in reported latency (that varied only by a few milliseconds) would have resulted in large overestimations of the calculated speed. Therefore, while the overall pattern of results stand, the exact speed values reported here should only be considered as estimates. We are also confident about our consistent finding of a non-linear decrease of foveal wave speeds in both BR and GFS. In further support of this decrease in wave speed, several observers

reported seeing waves slowing down until they stagnated and flipped back to the top of the stimulus during experiment 2.

The dissimilarity between the foveal and peripheral disappearance durations, and the finding that waves slow down as they propagate towards the fovea, was surprising and in need of some explanation. The most obvious possibility was cortical magnification - the amount of brain tissue in the occipital lobe responsible for foveal visual processing is much larger than that for peripheral processing (Tootell, Silverman, Switkes, & De Valois, 1982; Horton & Hoyt, 1991; Engel, Glover, & Wandell, 1997; Sereno, Dale, Reppas, Kwong, Belliveau, Brady, Rosen, & Tootell, 1995; Duncan & Boynton, 2003; Larsson & Heeger, 2006). Related to this difference in cortical representation are neuronal receptive field (RF) sizes. Neurons that represent the fovea have significantly smaller RFs than neurons in the periphery in each of the brain areas V1, V2, V3, and V4 (Dow, Snyder, Vautin, & Bauer, 1981; Smith, Singh, Williams, & Greenlee, 2001). It is possible that these neuronal characteristics underlie the wave's substantial deceleration when it is propagating towards the fovea. As the results in experiment 2 show, however, the cortical magnification factor can only explain a small fraction of the observed deceleration. The cortical magnification factor varies substantially between subjects (Duncan & Boynton, 2003) and could as such have been exceptionally prominent in all subjects. Although we cannot exclude this possibility, the total number of 11 different observers that performed in experiments 2, 3 and 5 makes it very unlikely that all observers' cortical magnification factors in V1 deviated strongly from the mean. Therefore, it appears that feedback from higher cortical areas or long range lateral connections within visual cortex may also play a role (Bringuier, Chavane,Glaeser, & Frégnac, 1999; Grinvald, Lieke, Frostig, Hildesheim, 1994). Lee et al., (2007) concluded that attention plays an important role in promoting the V1 neural activity of waves to higher visual areas. Given that waves travel faster in the absence of attention (Lee et al., 2007), it is tempting to suggest that when waves enter the fovea and the spatial acuity becomes higher, attentional processes further reduce the spread of activity in V1. Unfortunately, it is only possible to speculate as to the likely causes of the observed visual field anisotropies and inducer dependencies in wave propagation. Exactly how the brain's complex networks of distributed neural assemblies coordinate and generate transitions in perceptual awareness, remains one of the biggest mysteries in visual neuroscience. Adding further complexity to this question, a recent study found that the relative contribution of factors such as thalamic and lateral inputs can vary considerably depending on the

strength of sensory input (Nauhaus, Busse, Carandini, & Ringach, 2009). Luckily, the fact that BR and GFS provide a means to experimentally control and measure the dynamics of perceptual transitions, suggests these phenomena may be ideal for further exploration of this question.

Our finding that inducer strength can influence propagation speed and initiation probability complements recent work showing that the spatial origin of traveling suppression waves can be predicted by contrast, spatial frequency, and motion of the inducer (Paffen, Naber, Verstraten, 2008). It is interesting to speculate whether there is any functional significance to these systematic effects of inducer strength on the rapid propagation of new perceptual information at the expense of the previously perceived stimulus. As features such as stimulus contrast are known to be relevant to measures of visual salience, the increase in suppression wave propagation speed may be one reason why salient features appear to reach awareness faster than non-salient features of the environment. Contemporary theories have not yet linked visual saliency and suppression together so further experiments are needed to investigate how, and to what extent, the dynamics of suppression waves relate to other visual processes known to be influenced by the salience of visual features.

The similar pattern of results obtained in the GFS and BR experiments presented here, provides strong evidence that they may share the same underlying mechanism. Confirming whether or not there is only one means by which sensory information is temporarily rendered inaccessible to consciousness, is clearly critical for accurate interpretation of future research into the neural correlates of unconsciousness. Again, more work is needed before any conclusions can be drawn on this point. If further testing continues to reveal such large individual variation in the speed and strength of suppression waves as that observed here, individual differences may provide one avenue through which to investigate the relationship between these different phenomena.

The current study focused on BR and GFS, however, there are many other methods known to render stimuli consciously unavailable (for review, see Kim & Blake, 2005). With increasing effort being directed to these investigations, it is hoped that this study will shed light on why and how stimuli are rendered unconscious. The finding that dynamics of suppression waves vary as a function of inducer strength and direction of propagation relative to the fovea suggests a possible involvement of cognitive factors (attention), or a role for specific neural populations (feedback or long range lateral connections) in constraining the

transitions between perceptual awareness and suppression. The recent finding that visual phantoms also propagate in a similar wave-like manner (Meng, Ferneyhough, & Tong, 2007), raises the exciting possibility that these widely varying visual phenomena are all tapping into the same basic mechanism.

8. Acknowledgements

9. References

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