Mapping a field of suppression surrounding visual stimuli

Mark Chappell

The brightness of a small incremental flash was found to be considerably suppressed in the vicinity of a moving visual stimulus (effect size, d, up to 6) and less so around a stationary stimulus. The pattern of suppression was mapped and extended 3.5\degree away from a stationary stimulus and 10.5\degree behind, and ahead of, a moving stimulus. A second experiment found that dark flashes appeared less dark in the presence of an inducing stimulus of either polarity. Combined results suggest that perceived contrast was being suppressed, in all cases by an inducing stimulus of lesser contrast, and in most cases by an inducing stimulus of lesser luminance. These findings were compared with a number of recent models of the perception of the position of moving visual stimuli. These assume that in the wake of such a stimulus, at certain retinal or cortical areas, there is a region of neural inhibition and that, preceding them, there is a (bow-wave-like) region of neural excitation. The current findings confirm the inhibitory, but not the excitatory, assumptions in these theories.

Keywords: motion, flash, suppression, brightness, range, contrast–contrast induction, gain control, inhibition


Introduction

A number of recent studies have investigated the effect of moving visual stimuli on the visibility of other stimuli in their vicinity. Bonneh, Cooperman, and Sagi (2001) and Wilke, Logothetis, and Leopold (2003) found that a field of moving dots caused stationary dots to be periodically invisible. Takeuchi and De Valois (2000) showed that surrounding a stationary grating with a drifting grating reduced the perceived contrast of the stationary grating, although if the internal grating was also moving, enhancement of its contrast was also possible. This latter work extends a large body of research with stationary or flickering gratings (reviewed by Petrov & McKee, 2006; Series, Lorenceau, & Frégnac, 2003; Xing & Heeger, 2001), revealing the operations of a contrast gain control mechanism (e.g., D’Zmura & Singer, 1999; Schwartz & Simoncelli, 2001).

However, there seems to have been little study of such effects around a single, spatially compact, moving stimulus and, in particular, of the spatial extent of such effects. MacKay (1960) reported that moving his finger behind a glowing wire tended to render the latter invisible, an effect that was more formally investigated by Grindley and Townsend (1966). But only Morland, Ogilvie, Ruddock, and Wright (1996), in a case study of an individual with color perception deficits, seem to have mapped the range of such effects. They reported suppression of grating detection 20\degree ahead of a moving stimulus.

Experiment 1 of this study found that the brightness (i.e., perceived luminance) of a small flash was suppressed in all directions around a moving rectangular stimulus, hereafter called the inducing stimulus. The pattern of variation of this suppression was mapped in a large region around the inducing stimulus by systematically varying the position of the test flash (see Figure 1). The brightness of the test flash was measured by comparison with a reference flash remote from the moving inducing stimulus. Control conditions had a stationary inducing stimulus or no inducing stimulus. In Experiment 2, a single location was surveyed, using all four combinations of inducing stimulus and test flash polarities.

Experiment 1

Methods

Participants

Five naive participants were tested (during piloting of the stimuli, data from the author showed the same pattern as that found with these participants). All received a small reimbursement for their expenses in attending, and one also received some course credit. Four were male, and all had normal or corrected-to-normal vision.

Apparatus

Viewing distance was 57 cm from a 15-in. CRT, with a refresh rate of 60 Hz. Ambient lighting was dim (<0.3 cd/m\(^2\), Tektronix J18 1\degree luminance probe).
Stimuli and procedure

Figure 1 details the stimulus arrangement. On each trial, a gray test flash (1.3° × 1.3°) appeared at one of the positions above the dashed line (the latter was not displayed to the participants). The same gray-scale level (45 on a 0–63 scale) was used for all test flashes, but because of variation across the screen, their luminance occupied the 38- to 48-cd/m² range. As suppression was measured relative to a control condition where there was no inducing stimulus, these variations were controlled for (no gamma correction of the luminance scale was performed, but no plausible monotonic transformation could substantially change the pattern of the results). The luminance of the uniform gray background was below the resolution of the probe: <0.3 cd/m².

Participants compared the test flash’s brightness with that of a simultaneously presented gray reference flash of the same size, which was always vertically below it, and indicated via a button press (“up” or “down” arrow keys) which flash was brighter. For trials on which they could not discriminate the brightness of the two flashes, they were instructed to attempt to respond “up” and “down” equally often. They pressed “e” to indicate a key-press error. Time out occurred 1,500 ms after the inducing stimulus disappeared. On different trials, a range of luminance settings for the reference flash were tested, in an adaptive method of constant stimuli (Chappell & Hine, 2004), to find a setting for which its brightness was subjectively equivalent to that of the test flash (cf. Breitmeyer et al., 2006; Ögmen, Breitmeyer, & Melvin, 2003; Sheth, Nijhawan, & Shimojo, 2000). The reference flash luminance setting, determined as above and represented by its gray-scale index (0–63), was the dependent variable.

Luminance settings of the reference flash were determined in this way with three different inducing stimulus arrangements. In the first, there was a gray inducing stimulus moving horizontally at 15°/s (half of the trials, left to right; the other half, right to left; size, 4.5° × 1.3°; luminance, 20–22 cd/m²), as shown in Figure 1. This measure of the apparent brightness of the test flash will be represented by \( B_{MO} \). In the second arrangement, the same inducing stimulus was stationary in the position shown in Figure 1 (\( B_{SO} \)). Finally, as a baseline, the brightness comparisons were carried out in the absence of any inducing stimulus (\( B_{NO} \)). In conditions with an inducing stimulus, it was visible for 900 ms before the flashes appeared.

The difference in the reference flash luminance settings required for subjective brightness equality with the test flash, between trials in which there was a moving or stationary inducing stimulus and trials in which there was no inducing stimulus, provided a measure of suppression, or enhancement, at the positions tested (in gray-scale units).

The center of the inducing stimulus in Figure 1 was the center of the coordinate system. The moving stimulus occupied this position in the frame in which flashes appeared. Horizontal positions were as follows (inducer–test separations are enclosed in parentheses): −11.8 (10.5), −8.3 (7.0), −4.8 (3.5), −1.4 (0.1), 1.4 (0.1), 3.3 (2.0), 5.3 (4.0), and 11.8° (10.5°), respectively, for the test flashes in the top row of Figure 1. For the bottom three rows of test flashes, vertical positions were 3.0 (0.1), 5.0 (2.1), and 7.0° (4.1°), respectively (downward direction positive). The reference flash was at \( Y = 10.5° \). For trials on which the flashes were ahead of the moving stimulus (indicated by vertical dashed line [not displayed]), participants fixated a point at \( X = 7.65° ± 1° \). On other trials, this white fixation cross was behind the moving stimulus when the flashes appeared (\( X = −6.65° ± 1° \); so that the inducing stimulus never interposed between the fixation and the test flash). Around each of these locations, the fixation point occupied a range of positions in a horizontal random window 2° wide so as to somewhat spread the activation due to repeated trials over the retina.
Only one fixation cross was visible on a given trial (88–105 cd/m², \( Y = 6^\circ \)).

As already previewed, suppression was found both behind and ahead of the moving visual stimulus. Potential contributions to this effect would be processes associated with the inducing stimulus crossing the space occupied by the test flash, before the test flash appeared in the former case or after it appeared in the latter (forward or backward masking). In an attempt to quantify such effects, for a limited number of the test flash positions in Figure 1, trials also occurred in which the test flash occupied a portion of the space that the inducing stimulus also occupied, but the test flash was displayed before or after the inducing stimulus appeared (\( B_{TO} \)). The inducing stimulus was displayed for approximately the time the moving stimulus took to traverse the space occupied by the test flash (100 ms), in other trials where a moving inducing stimulus did appear. The temporal offsets approximated the time it took the moving stimulus to travel from the test flash position to the position it is shown occupying in Figure 1 (−750, −500, −250, +133, +267 ms).

All conditions for horizontal half-rows of test flash positions (including the temporal offset conditions), either to the left or to the right of the vertical dashed line in Figure 1, were tested in a single block. (Some blocks [two for P3, one for P4, and three for P5] were retested, and in one case, data were merged across sessions to achieve a reliability criterion [confidence interval size < 18]. Both of the \( Y = 0^\circ \) blocks of P1 were retested because the content of these blocks was modified slightly for later Ps.)

**Results**

Figure 2 shows results from all conditions tested. Most data points are based on approximately 54 trials per participant (a minimal number timed out).

**Control conditions**

Comparing the stationary inducing stimulus conditions (Figure 2, green data) with the no-inducing stimulus conditions (Figure 2, blue data) revealed...
conditions (blue) reveals significant (as indicated by nonoverlap of 95% confidence intervals) suppression for test flash positions adjacent to the inducing stimulus for most participants, but generally speaking, this suppression does not extend far from the stimulus. Figure 3 (SO) shows average brightness suppression data for these conditions (i.e., differences between the stationary inducing stimulus and the no-inducing stimulus conditions \(B_{SO} - B_{NO}\), or green data – blue data in Figure 2) were computed for each participant, then averaged). Across participants, suppression was also significant adjacent to the inducing stimulus but \((X = 3.3, Y = 0, 2° separation)\) was the only nonadjacent point where it was significant (95% confidence interval not crossing the X-axis).

A similar treatment for “temporal offset” conditions \((B_{TO} - B_{NO})\) indicated that having a stationary inducing stimulus “overwrite” the test flash did not suppress its brightness (Figures 2 [purple] and 3 [Temp], positive X) at the temporal offsets tested. However, the inducing stimulus appearing prior to the test flash, in the location the test flash subsequently occupied, had a suppressive effect (Figures 2 [purple] and 3 [Temp], negative X).

**Suppression due to moving inducing stimulus**

Comparing the moving inducing stimulus conditions (red) with the no-inducing stimulus control conditions (blue), it is evident that there is substantial brightness suppression in the regions around a moving stimulus. The top row of Figure 2 indicates that for all participants, statistically significant suppression extended to at least 5° behind the moving stimulus, and for three participants, it extended 3° ahead. The second row indicates that significant suppression also extended to two positions just to one side of the moving stimulus’ path, adjacent to it, and just behind it, for four out of five participants. At no testing position did any participants’ data approach significant enhancement (red above blue). Figure 3 (right panels, P1–P3) displays the patterns of suppression due to a moving inducing stimulus \((B_{MO} - B_{NO})\) or red data - blue data in Figure 2), across the visual space tested, for three representative participants (data have been reflected through a plane bisecting the inducing stimulus, along its trajectory, and vertically out of the page in Figure 1; interpolation between testing points was via Matlab interp2(), with interpolation type bicubic).

**Figure 3 (MO)** shows the average suppressive effect due to a moving inducing stimulus \((B_{MO} - B_{NO})\) across the five participants. The remarkable consistency of this effect across participants resulted in significant suppression at the great majority of all test flash positions tested, with only five participants. It is also of note that the suppression identified here had substantial magnitude—the average immediately behind the moving stimulus was 19 gray-scale levels. This point is further emphasized by Table 1, which shows effect sizes for the suppressive effects estimated from the five participants (except for some peripheral positions that were not tested with later participants), recalling that 0.8 indicates a large effect size (Cohen, 1992).

**“Pure” motion**

One may also inquire as to what portion of the brightness suppression around the moving inducing stimulus is additional to that around a stationary stimulus. Subtracting results for a stationary inducing stimulus from those for moving inducing stimuli \((B_{MO} - B_{SO})\) addresses...
this question, and Figure 3 (MO − SO) shows average differences. Along the axis of motion (Y = 0), a significant effect of motion per se is in evidence behind the moving stimulus but only at one position ahead of it. Significant effects were also found at numerous testing positions beside the motion trajectory, notably at two positions where the separation between the inducing and test stimuli was 2°.

Suppression behind the moving stimulus, however, might also be attributed to the forward masking effect of the moving stimulus traversing the space later occupied by the test flash. Figure 3 (MO − Temp) shows the result of subtracting luminance measures for moving inducing stimuli and temporally offset stimuli (BM0 − BT0). It reveals that, so far as this masking effect has been operationalized, behind the moving stimulus, the masking can only be distinguished from suppression due to motion at Y = −11.8°.

Discussion

Simultaneous brightness induction

The primary interest here was to investigate brightness suppression around a moving visual stimulus. However, the stationary inducing stimulus conditions included as a control require some mention. They revealed significant brightness suppression in a small region adjacent to the stationary stimulus. According to Heinemann’s (1972) review, simultaneous brightness induction—where two patches of different luminance are displayed in the vicinity of each other and where their luminance difference is exaggerated in the visual system—has a similar range of about 2°, although with very bright inducing stimuli McCann and Savoy (1991) did find simultaneous brightness induction for inducer–test separations out to 7.5°.

In any case, Experiment 1 sought to make simultaneous brightness induction a counter-confound—the moving and stationary inducing stimuli were substantially less luminous than the test flashes, as measured on persisting patches. Thus, any brightness induction should have made the test flashes appear brighter. However, it is conceivable that, because of their different temporal properties, the test flashes might have been perceived to be dimmer and that the relative brightnesses might be crucial in determining the direction of contrast effects. For short flashes (up to about 100 ms, Whittle, 1994), Bloch’s law states that brightness is related to the product of time and luminosity increment. Participants were thus recalled to the laboratory to compare the brightness of the moving inducing stimulus to that of the reference flash and, in another condition, the brightness of a stationary inducing stimulus to that of the reference flash. In both cases, there was no test flash present.

The black data in the top row of Figure 2 show the results (□ = stationary inducing stimulus; Δ = moving inducing stimulus). Only P5 perceived the test flash to be significantly dimmer than the inducing stimuli (and then only for one test flash position). Thus, it seems that different processes underlie simultaneous brightness induction and the brightness suppression effect revealed here (Figure 2 shows that for three participants, the moving stimulus was perceived to be significantly dimmer than the test flashes, as in fact it was. Brightness assimilation might have “pulled” the brightness of the test flashes toward that of the inducing stimulus. However, such assimilation effects are usually only observed with high spatial frequency stimuli; Blakeslee & McCourt, 2004; Fiorentini, Baumgartner, Magnussen, Schiller, & Thomas, 1990).

Masking

In the temporal offset conditions, no effect was found of the inducing stimulus overwriting the test flash—there was no backward masking. However, the inducing stimulus significantly suppressed the brightness of a test flash, which later occupied a subset of the space it occupied—forward masking. This is seemingly at odds with Ögmen et al.’s (2003) finding greater backward than forward masking. However, their stimuli were very different—an annular mask whose inner boundary coincided with a circular test stimulus—with both stimuli being presented as flashes. Breitmeyer and Ögmen (2006) point out that such stimulus differences are important, and their effects have not been fully explored. Further, Ögmen et al.’s backward masking was maximal with an SOA of about 50 ms and much reduced at 100 ms. Because the stimuli spatially overlay each other, the minimum SOA used in the current work was 133 ms in this direction. In the forward-masking direction, the minimum SOA was 250 ms in this study. At this SOA, Ögmen et al. found small but still significant forward and backward masking, of roughly equal magnitudes.

Summary

Comparisons between the moving inducing stimulus conditions and various control conditions revealed that forward masking may account for the suppression found behind the moving stimulus and that the presence of an inducing stimulus per se (i.e., stationary) accounts for the suppression at some adjacent test flash positions, and most in front of the moving stimulus.

This left six positions to the side of the moving stimulus and one in front of it as testing positions where the suppression could unambiguously be attributed to the motion attribute of the inducing stimulus. For positions to the side, which were passed by the moving stimulus before the test flash appeared, it is possible that there is a residual inhibitory effect remaining from that earlier time. The dynamics of decay of suppression (cf. van der Wildt & Vrolijk, 1981; Vrolijk & van der Wildt, 1982, 1985) need to be determined to assess this contribution.
The original focus of this article, however, was not on suppression due to “pure” motion but on any suppression (regardless of source) that might surround a moving stimulus, and this was found to be substantial and extensive. The range, extending to test flash–inducer separations of 10.5° both behind and in front of the moving inducing stimulus, is at least as great as that found with the brightest inducing stimuli in a simultaneous brightness induction paradigm (McCann & Savoy, 1991).

The shape of the suppression behind the moving stimulus, revealed in Figure 3, is very reminiscent of a brightness induction paradigm (McCann & Savoy, 1991). With the brightest inducing stimuli in a simultaneous moving inducing stimulus, is at least as great as that found with the brightest inducing stimuli in a simultaneous brightness induction paradigm (McCann & Savoy, 1991). However, to the extent that there is a bow wave, it is a depression, rather than the elevation seen in front of a boat. The theoretical implications of these findings are considered in the General discussion section, but first, they are supplemented with a brief investigation of the effect of reversing the polarity of the stimuli (as suggested by anonymous reviewers).

**Experiment 2**

Experiment 2 surveyed the effect of all four combinations of inducing stimulus and test flash polarity at a single test flash location. This position was chosen because effects at this position were substantial in Experiment 1, but it was out of the path of the moving inducing stimulus and somewhat remote from it, thus easing interpretation.

**Methods**

**Participants**

Data from eight naive participants are presented. However, as detailed below, data are missing for some blocks, for three participants. All received a small reimbursement for their expenses in attending. Seven were female, and all had normal or corrected-to-normal vision.

**Apparatus**

Viewing distance was controlled, via a chin rest, at 76 cm from a 15-in. CRT. The monitor refresh rate was 85 Hz. Ambient lighting was brighter than that in Experiment 1 (in part to reduce afterimages of the boundary between the relatively bright background on screen and its border)—~13 cd/m² on the wall behind the monitor.

**Stimuli and procedure**

The test flash position marked with an “X” in Figure 1 was that surveyed in this experiment (~4.8, 3). Toward the end of piloting the stimuli, the author experienced intermittent mild discomfort in one eye, which might also have been due to, or exacerbated by, poor health at the time. Participants were informed of this risk—none reported any discomfort. To reduce the risk of visual discomfort, the hardware was altered to produce an 85-Hz refresh rate. Subsequent retuning of the stimuli included exposing test and reference flashes for two frames but reducing their size to 0.8° × 0.8°.

Table 2 shows the stimulus luminances used in Experiment 2. In choosing luminances for the dark stimuli, I sought (a) to maximize the contrast of the inducing stimuli with the background, so as to maximize the effects measured; (b) not to have too bright a background, as this might contribute to visual discomfort; (c) not to use too dark a test flash, so that at least some reference flashes would appear reliably darker than it for most participants; and (d) to use a test flash that was, and which appeared, darker than the inducing stimulus. The main background extended 10° above fixation and 6.5° below it and had a luminance of 32 cd/m² at its center. Small strips of the screen above and below this area had a luminance of 12 cd/m². The white fixation’s luminance was 107–110 cd/m².

Four main blocks of conditions were tested. In each block, a particular combination of test flash and inducing stimulus brightness was used: dark–dark, dark–bright, bright–dark, and bright–bright. Within each block, there were three conditions: no inducing stimulus, stationary inducing stimulus, and moving inducing stimulus. A final block involved brightness comparisons between a dark test flash and a dark inducing stimulus, whether stationary or moving.

Points of subjective brightness equality were computed as for Experiment 1. As only one location was being surveyed, a more stringent reliability criterion of <8 was adopted (comparable to the accuracy achieved for this location in Experiment 1). Data for blocks for which this was not achieved for all conditions are not presented. Participant data points are based on at least 54 trials but often more for the dark test flash blocks, which all participants found more difficult.

**Results**

Figure 4 shows individual and average brightness match data for all four stimulus brightness combinations. (Data are missing for Participant 3 for the dark flash–bright

<table>
<thead>
<tr>
<th>Stimulus</th>
<th>Dark (L°/L°)</th>
<th>Bright (L°/L°)</th>
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<tbody>
<tr>
<td>Inducing</td>
<td>8 (0.75)</td>
<td>53 (0.66)</td>
</tr>
<tr>
<td>Test flash</td>
<td>5 (0.84)</td>
<td>57 (0.78)</td>
</tr>
</tbody>
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Table 2. Luminances (cd/m²) used in Experiment 2 (contrasts are enclosed in parentheses; (L° − L°)/L°).
inducing stimulus block, as the test flash was too frequently perceived as darker than the reference flash, even at the latter’s darkest setting [although convergence was achieved in the dark flash–dark inducing stimulus block]. This points to the possibility of habituation as testing proceeds, as a function of what inducing stimuli are appearing. The accuracy criteria could not be achieved with dark flashes for Participant 7, but the pattern of her data was the same as that of the average, in both these conditions. Participant 8 withdrew due to ill health after one testing session. In addition to the blocks that are reported, she was also tested on the dark–dark block but did not meet the accuracy criterion. This was the only excluded block for which a difference between conditions opposed a difference found to be significant. The effect of reincluding Participant 7 and 8’s data is noted below.)

For the dark flash–dark inducing stimulus conditions, the stationary inducing stimulus did not significantly change the test flash’s brightness, but the moving dark inducing stimulus did result in the test flash appearing significantly less dark, \( t(5) = 4.0, p = .01 \). The difference between moving and stationary inducing stimuli was also significant, \( t(5) = 3.5, p = .02 \). (If P7 and P8 data were included in this analysis, the significance of the first comparison would be unchanged, whereas the second comparison would have increased to \( p = .002 \).)

Figure 4 also shows that when participants rated the brightness of the inducing stimulus (Cf. Stat or Cf. M), they perceived it to be much brighter than the test flash (No TS), stationary: \( t(5) = 4.7, p = .005 \); moving: \( t(5) = 4.5, p = .006 \).

For the dark flash–bright inducing stimulus conditions, the moving inducing stimulus, as compared with no inducing stimulus, just reached significance, \( t(5) = 2.57, p = .0498 \)! (A Wilcoxon signed rank test, which discounts the effect of P6’s outlying difference on the error variance, confirms that the difference is reliable, \( Z = 2.2, p = .03 \). If P7’s data were included in this analysis, using a value of 0 for the “no-inducing stimulus” condition, for which the logistic regression returned—0.33, the significance of this difference would have increased.)

No significant inhibitory (or excitatory) effects occurred with the bright flash–dark inducing stimulus conditions. Finally, for the bright–bright conditions, both inducing stimuli significantly reduced the flash’s brightness, stationary: \( t(6) = 2.6, p = .04 \); moving: \( t(6) = 3.1, p = .02 \), but there was no difference between moving and stationary inducing stimuli.

Discussion

For the dark–dark conditions, simultaneous brightness induction was ruled out in the same fashion as in Experiment 1. The test flash was less luminous than the inducing stimulus and was rated as significantly less bright by participants, and thus, brightness induction should have made it darker, not brighter, as was observed. The flash was also longer in Experiment 2, which would have increased the darkness of dark flashes.
The dark flash–bright inducing stimulus condition, where the dark flash was significantly less dark in the presence of an inducing stimulus that was more luminous than the background, was even more conclusive regarding this issue. Effects were smaller than those in Experiment 1, at the same location \((d = 1.2\) for bright–bright condition), in part no doubt because the inducing stimulus had less contrast in Experiment 2. Perhaps because of this, the difference found in Experiment 1 between the effects of stationary inducing stimuli and those of moving inducing stimuli was not found in the bright–bright condition, although it did replicate in the dark–dark condition. In summary, all polarity conditions, except for the dark flash–bright inducing stimulus one, showed a significant suppressive effect due to a moving inducer—the brightness of bright flashes and the darkness of dark flashes were suppressed. However, only the bright–bright condition revealed a suppressive effect due to a stationary inducer. As the test–inducer separation here was 3.5°, this nevertheless revealed a greater range for this effect than was found in Experiment 1.

**General discussion**

In Experiment 1, very large suppressive effects were demonstrated in all directions around a moving visual stimulus. Indeed, the estimates above should be regarded as lower bounds on the magnitude of the suppression, as it is entirely possible that the brightness of the reference flash was also suppressed by the inducing stimuli, thus reducing the difference in apparent brightness between it and the test stimulus.

Experiment 2 generalized this, finding smaller but significant suppressive effects on a dark test flash due to an inducing stimulus of either polarity. Stimulus properties were again such that simultaneous brightness induction should have produced effects in the opposite direction to those found. However, when suppressive effects occurred in Experiment 2, the flash’s brightness moved toward that of the background, from both the dark and bright “sides”. This suggests an account in terms of contrast suppression (thanks to an anonymous reviewer for this observation). In what follows, the results in the current work will first be compared with research on this phenomenon, then with other related empirical findings, and finally, some theoretical implications will be considered.

**Comparison to other empirical results**

**Contrast–contrast induction**

When a test patch of sinusoidal luminance grating is adjacent to an inducing grating with the same average luminance, but different contrast, the perceived contrast of the test patch may be suppressed or enhanced, compared to its perception alone, depending on stimulus parameters and test conditions (Ejima & Miura, 1984; Ejima & Takahashi, 1985; Sagi & Hochstein, 1985; Tolhurst & Thompson, 1975)—such effects also occur with randomly checked texture patterns (Chubb, Sperling, & Solomon, 1989). Findings depend, to an extent, on whether the induction is measured with contrast thresholds (detection or increment), temporal nulling, or matching (reviewed by Petrov & McKee, 2006; Xing & Heeger, 2001)—findings with the last method will be emphasized here.

With contrast matching, suppression is greatest when the inducing contrast is much greater than that of the test. It is reduced, but may still be apparent, for inducing contrast slightly less than the test, for a test grating that is foveally centered (e.g., Cannon & Fullenkamp, 1991; Xing & Heeger, 2000, 2001). One may also get enhancement of test contrast when its contrast is greater than the inducer’s (e.g., Ejima & Takahashi, 1985; Snowden & Hammett, 1998). As they moved test and inducer into peripheral vision, Xing and Heeger (2000) found that suppression increased considerably and that there was no enhancement under any conditions at 10° eccentricity. Indeed, at this eccentricity, Xing and Heeger (2000) found significant suppression with an inducing contrast of 0.2, which was much less than the test patch contrast of 0.8. Computing the contrast of the stimuli in this study as \(\frac{L_s - L_B}{L_B}\), in all cases, the inducing stimulus had less contrast than the test flash (see Table 2 for Experiment 2 values). However, as in most cases the test flash was outside the fovea, the finding of suppression only in the current work was consistent with the contrast–contrast suppression literature.

The range of contrast–contrast effects has been assessed in a number of ways. In common with much of the work in this area, Cannon and Fullenkamp (1991) used a circular test patch surrounded by an annular inducing patch. They varied the width of the inducing annulus and found that increasing the width beyond 2.5° was still measurably increasing the suppression. Xing and Heeger (2001) similarly found that changing their inducing annulus width from 1.75° to 4.25° increased suppression.

D’Zmura and Singer (1999) reviewed a number of their previous studies in which they modulated in space and time the contrast of a surround with a binary texture and wherein participants nulled the induced temporal modulation of the center test. Inverse Fourier transforming suppression as a function of spatial frequency, they computed a range of 2–3° for suppression.

Using a third method, manipulating the width of an annular gap between center and inducer, Cannon and Fullenkamp (1991) found significant suppression out to their maximum gap width of 1.2°. Petrov and McKee (2006) used a similar arrangement but measured detection thresholds. The work of Petrov and McKee is mentioned because their study and the study by Wilkinson, Wilson, and Ellemberg (1997) described below are the only...
studies, of which I am aware, which have investigated the effect of separation for stimuli in the periphery. They found the space constant (wherein the suppression fell to $1/e$ of maximum) to increase from $\sim 0.7^\circ$ to $\sim 1.4^\circ$ as eccentricity increased from $2.7^\circ$ to $11^\circ$. Consideration of their Figure 3 (Petrov & McKee, 2006, p. 231) suggests a range of a little over $3^\circ$ at $2.7^\circ$ eccentricity, whereas at $11^\circ$ eccentricity, suppression appeared to extend beyond the $4.5^\circ$ they tested.

Finally, with a linear array of Gabors, Wilkinson et al. (1999) found that the increment threshold for the central Gabor, whose eccentricity was $5.7^\circ$, was elevated for separations out to about $2^\circ$.

Thus, as measured with matching, contrast–contrast suppression has a range of at least $2^\circ$, for a foveal target. Other methods suggest that, in the periphery, its range is greater, but on the other hand, when inducing stimuli not surrounding the test patch are used, the range is reduced for foveal (Cannon & Fullenkamp, 1996) and peripheral (Wilkinson et al., 1997) targets—exactly how these two factors would trade off is unclear. A range of $2^\circ$ is comparable with the range of the effect around a stationary inducing stimulus in this study.

All of the above work dealt with stationary or flickering stimuli. Takeuchi and De Valois (2000) used a drifting inducing grating and found suppression or enhancement of the apparent contrast of a stationary or moving test grating, depending on conditions. They also examined the effect of separation but only tested for, and found, effects out to $0.4^\circ$, for foveally centered targets.

In short, comparison with the contrast–contrast suppression literature suggests that the current studies may well be measuring a variant of this effect, albeit with novel methods. While experiments in the contrast–contrast area have generally equated the average luminance of inducing and test areas, in most cases, the luminance of the inducing stimulus in this study differed from that of the test in a direction so as to oppose simultaneous brightness contrast, so that this potential confound was even better controlled (cf. Yu, Klein, & Levi, 2001). Further, the inducing contrasts in the current work were always lower than those of the test stimulus, which is not optimal for contrast–contrast suppression. These facts, together with the greater range I have found, particularly with a moving inducer, suggest that my method, with a suprathreshold but brief test stimulus, is more sensitive and/or is probing a different process (see the Neural inhibition section).

### Theoretical implications

#### Contrast gain control and pathways

Contrast–contrast suppression has often been seen as a gain control mechanism, which allows the visual system to handle a greater range of input by restricting the input to certain detectors to their nonsaturated domain (e.g., Petrov & McKee, 2006; Schwartz & Simoncelli, 2001; Solomon, Sperling, & Chubb, 1993). As Meese and Holmes (2007) and Zemon and Gordon (2006) have pointed out, gain control is likely to be more necessary in the M pathway, which saturates, than in the P pathway, where responses are close to linear for all inputs. Consistent with this, the M pathway is likely to be involved in processing the moving inducer and flashed test stimuli in the current study (Livingstone & Hubel, 1987).

#### Neural inhibition

It is also often argued that neural inhibition underlies contrast suppression (e.g., Xing & Heeger, 2001). Even when Polat and Sagi (1993) found lowered thresholds for detection of contrast, they argued that it might be due to neural inhibition of noise. Thus, a plausible candidate for a process underlying the suppression measured here would be inhibition of the neurons responsible for the perception of the contrast of the flash, by other neurons involved in processing the moving or stationary inducing stimulus.

The suppression across polarity found in Experiment 2, at least, is likely to be happening at the cortical level, as ON and OFF channels are thought to be largely separate.
up to that level (Fiorentini et al., 1990; Schiller, 1992). Notably, results of testing for interocular transfer in contrast–contrast suppression have been mixed (Chubb et al., 1989; Petrov & McKee, 2006; Singer & D’Zmura, 1994), leading to controversy regarding cortical involvement. The large range of suppressive effects in this study further suggests the involvement of inhibitory feedback from higher visual areas to primary ones (cf. Angelucci & Bullier, 2003; Shapley, 2004).

Speculatively, then, the method described here may be probing long-range neural inhibition, associated with the M pathway, and mediated at the cortical level, but more direct experimental confirmation is required.

Models of perception of moving stimuli

Assuming that reduced neural activation, whether due to inhibition or habituation, was responsible for the observed contrast suppression in this study, then the results presented here have applicability to assessing a number of models of moving object perception. For example, models proposed by Fu, Shen, and Dan (2001), Kanai, Sheth, and Shimojo (2004; also see Sheth et al., 2000), and Kirschfeld and Kammer (1999; also see Kirschfeld, 2006) assumed a region of inhibition in processing regions corresponding to positions behind moving stimuli (earlier similar proposals are reviewed by Breitmeyer & Ögmen, 2006). The results of the current study are in agreement with those models.

However, Kanai et al. (2004; also see Sheth et al., 2000) and Kirschfeld and Kammer (1999; also see Kirschfeld, 2006) also assumed a region of excitation to exist in visual processing regions corresponding to positions ahead of moving stimuli. One could argue that their posited excitation is somehow specific to that moving stimulus; that is, it can only affect that moving stimulus when it reaches the region of excitation. In that case, the flashes used here would not be appropriate probes of it. However, if this position is maintained, it may be difficult to falsify. One possibility is that the excitation may only facilitate processing of other moving stimuli—it may be possible to contrive a suitable test stimulus to test this (cf. Whitney et al., 2003). Alternatively, one might argue that the excitation is only effective in a very small region immediately in front of the moving stimulus, and that flashes in the current work were not spatially accurate enough to probe this. However, if this were the case, the excitatory region would have to switch within a quite small distance (≈0.5°) to an inhibitory region. Although this is possible, it seems more parsimonious to conclude that the data in this study do not support these models.

It is also of note that Glaser and Barch (1999) have proposed and simulated a neural model of visual motion processing that exhibits what they termed “bow waves” of activity. These are entirely excitatory. Unless the speed of the moving object is small compared to the speed of propagation in the network (Barch & Glaser, 2002; in which case excitation extends ahead of the moving object), the excitation forms two wakes trailing from the outside edges of the moving object (Glaser & Barch, 1999). Again, if neural inhibition underlies the suppression reported here, existence of such wakes is not supported.

Returning to Kirschfeld and Kammer’s (1999) model, their excitatory process served to provide an explanation of the flash-lag illusion, in which a moving stimulus displayed in alignment with a flash is perceived to spatially lead it (Krekelberg & Lappe, 2001; Nijhawan, 2002; Ögmen, Patel, Bedell, & Camuz, 2004; Schlag & Shlag-Rey, 2002; Whitney, 2002). According to Kirschfeld and Kammer, the excitatory process would allow the moving stimulus to be processed more quickly, at a given position, than the flash and, thus, would appear to spatially lead the flash. The present results suggest an alternative account. Objects displayed with less luminance are processed with a longer latency (e.g., Wilson & Anstis, 1969). More to the point, especially under conditions where the target has a shorter duration than (or is less luminous than) the mask, reaction times to targets may be increased by the presence of the mask, in a metac contrast or paracontrast paradigm (Breitmeyer & Ögmen, 2006; Kirschfeld & Kammer, 2000). Experimentation is needed to confirm my hypothesis that the flash-lag flash’s processing is slowed by the moving stimulus, thus providing an alternative basis for a differential latency account of this illusion.

Fields

The graphs in Figure 3 (and similar ones mapping spatial distortion around a moving stimulus [Watanabe & Yokoi, 2006] and attention [Gobell, Tseng, & Sperling, 2004; Tse, 2004]) suggest following an approach used extensively in physics and imagining that visual stimuli are surrounded by various fields, which may be probed and mapped using appropriate methods, somewhat akin to perceptive fields (Fiorentini et al., 1990). The perception of a second visual stimulus is then changed by an amount that may be predicted based on knowing the field strength at the point occupied by the second stimulus.

Conclusions

The contrast of a suprathreshold test flash was found to be substantially suppressed in an extensive region, particularly around moving visual stimuli. The range of the effects around stationary stimuli was consistent with that found previously for contrast–contrast suppression, but that around moving stimuli was much greater, and may reflect the operation of a process not probed by those studies, possibly associated with the M pathway. Assuming that the suppression is based on neural inhibition,
findings provide support for the inhibitory wake assumed in a number of models of visual motion perception (Fu et al., 2001; Kanai et al., 2004; Kirschfeld, 2006; Kirschfeld & Kammer, 1999; Sheth et al., 2000). However, support was not found for the assumption in some of these models (Kanai et al., 2004; Kirschfeld & Kammer, 1999; Sheth et al., 2000) that a region of excitation extends in front of a moving visual stimulus. Whitney and Cavanagh (2000, 2002) have shown that a moving stimulus influences the perceived position of other flashed and moving stimuli. The present work shows that such a stimulus also affects another attribute of flashes—their perceived contrast.

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**References**


