Phantom flashes caused by interactions across visual space

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Studies regarding the effects of context on the perception of a visual target's temporal properties have generally addressed the cross-modal integration of auditory context, within a functional or ecological (e.g., Bayesian) framework. A deeper understanding of contextual effects in temporal vision may be gained by drawing connections with the rich models of signal processing developed in the field of spatial vision. To bridge this gap, we investigate a purely visual version of the cross-modal "double-flash" illusion (L. Shams, Y. Kamitani, & S. Shimojo, 2000; J. T. Wilson & W. Singer, 1981). Here, a single target flash can be perceived as several flashes if it is presented in the context of multiple visual inducers. This effect is robust across conditions where the target and inducers are of opposite contrast polarity, in different hemifields, are non-collinear, are presented dichoptically, or are high-frequency Gabor patches. The effect diminishes when target–inducer distance is increased or when the target is moved toward the fovea. When the target is foveated, the effect can still be recovered if the inducers are placed at 3° distance. Finally, we find that multiple target flashes are not "merged" into a smaller number of perceived flashes when presented with singular inducers. These results suggest a cortical mechanism based on isotropic propagation of transient signals or possibly based on higher level event detection. Finally, we find that multiple target flashes are not "merged" into a smaller number of perceived flashes when presented with singular inducers. These results suggest a mechanism based on the propagation of transient signals and argue against the relevance of the cue integration model developed for the cross-modal version of the effect.

Keywords: temporal vision, illusory flash, transient, cue integration, visual event, space

Introduction

There has been extensive study of the influence of visual context on the perception of a visual target. In the main, these studies have concerned the *spatial* properties of the target. For example, physiological, computational, and psychophysical studies have delineated the ways in which visual context affects the detectability and the perceived position, orientation, color, or brightness of a target (Levitt & Lund, 1997; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Sengpiel, Sen, & Blakemore, 1997; Somers et al., 1998; Stemmler, Usher, & Niebur, 1995). However, much less is known about how the perceived *temporal* properties of a target can be affected by the visual context.

In the cross-modal domain, a number of studies have identified ways in which auditory stimuli can impact the number of times a visual target is seen to have flashed. A single transient flash accompanied by multiple beeps is often perceived as multiple flashes (Shams, Kamitani, & Shimojo, 2000); similarly, the temporal rate of a series of flashes is perceptually sped up by a series of beeps played at a higher rate (Gebhard & Mowbray, 1959; Myers, Cotton, & Hilp, 1981; Regan & Spekreijse, 1977; Shipley, 1964; Welch, DuttonHurt, & Warren, 1986). Given that such effects can be generated when target and context (inducer) are of different modalities, it ought to be possible to achieve a similar effect when target and inducer are of the same modality. After all, connectivity within the visual cortex is richer than the connectivity between the largely segregated auditory and visual systems.

Such a long-range visual–visual interaction has been described (Wilson & Singer, 1981) between visual stimuli positioned as far as 20° apart. Observers were asked to report whether the target disk had been presented in a

single steady flash or if it had flickered (flashed twice). They made significantly more errors when the number of times the target and distracter disks were flashed did not match. In other words, observers were more likely to see a single flash as flickering if the distracter flashed twice, and they were more likely to see two flashes as a single steady flash if the distracter flashed once. There have been few studies following up on this finding (Leonards & Singer, 1997; Wilson, 1987), and thus the parametric properties and scope of the effect remain largely unknown. In particular, this intramodal interaction has not been examined in light of the theoretical and neurobiological implications raised by the more recent cross-modal studies.

The effect found by Wilson and Singer was framed as variations of a target feature, namely, the presence or absence of flicker. Meanwhile, the multisensory experiments have generally been concerned with how the target stimulus is segmented into perceptual tokens, namely, as individual flashes. We adopt this flash-counting task to test the case when target and inducer are of same modality, i.e., vision. This allows us to directly compare the within- and cross-modal effects. Furthermore, the task offers us a more graded report of the phenomenon, allowing us to directly examine perceptual effect strength in the face of various stimulus manipulations.

Investigations of the cross-modal illusion have yielded theoretical insights by offering cue integration models embedded in a Bayesian framework. In this framework, information from independent sensory channels is integrated in a Bayesian near-optimal manner (Alais & Burr, 2004), so that the final outcome depends on the weighted sum of the reliability of the information from the independent information sources (cue independence). Certain asymmetries in the data obtained by Wilson suggest that the visual–visual effect may not fit the model of cue independence; however, a pair of studies yielded opposite directions of effect (Wilson, 1987; Wilson & Singer, 1981). Here, using a graded report, the present study reconciles the findings and identifies models that have the promise to account for the visual–visual effect.

Experiment 1: Basic effect of multiple inducers on a single target

The target was always a single flash at a less eccentric ("central") location, and the observer's task on a given trial was to report the perceived number of target flashes. We presented a varying number (0–4) of inducer flashes in the periphery across trials.

Methods

Observers

Observers were ten volunteers (4 females) from Harvard University, including one of the authors (DAW), with normal or corrected-to-normal vision. With the exception of DAW, all observers were naive as to the actual stimulus configuration and the purpose of the study. The study was approved by the Committee on the Use of Human Subjects in Research of Harvard University and all participants provided written informed consent.

Stimuli

The display consisted of two white disks flashed on a black background, each subtending 1.5° diameter. Target and inducer disks were positioned at 4° and 9° eccentricity below fixation, respectively (Figure 1a). Disk luminance was 76.6 cd/m^2 and the average luminance of the background was 0.05 cd/m^2, as measured by a digital
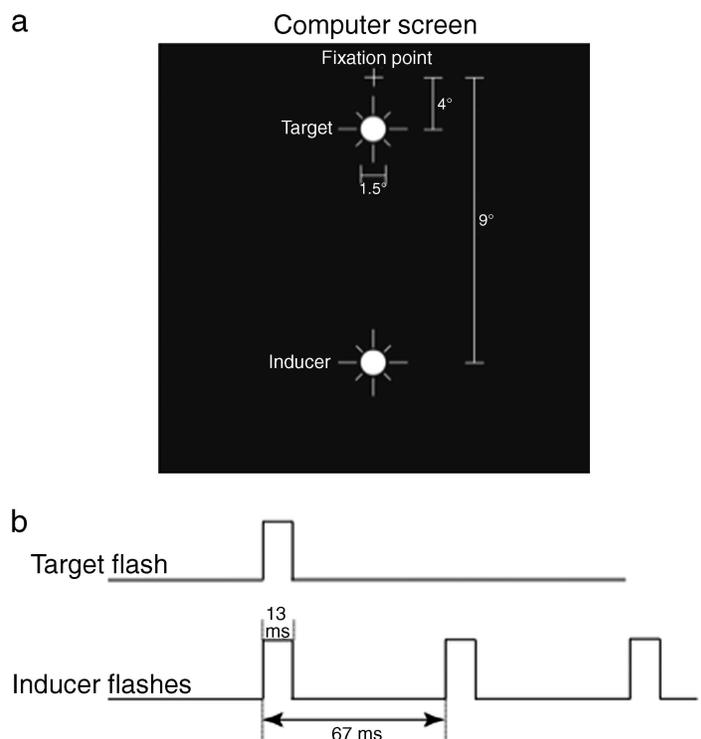

Figure 1. The spatiotemporal profile of stimuli in the main experiment. (a) The spatial configuration of the stimuli. The central stimulus was a circular disk of 1.5° diameter and its center was located at 4° eccentricity directly below the fixation point. The center of the peripheral stimulus was at 9° eccentricity directly below the fixation point. The distance between the two disks was 5°. Figure is not drawn to scale. (b) The temporal profile of the stimuli in one of the conditions (1 central flash, 3 peripheral flashes) is shown. The timings of the central and peripheral flashes were aligned at initiation.

photometer (Minolta Chroma Meter CS-100). The central disk flashed once for 13 ms. The peripheral inducer disk flashed, also for 13 ms, on a black computer screen 0, 1, 2, 3, or 4 times each, depending on trial, leading to a total of 5 conditions. The stimulus onset asynchrony (SOA) of successive flashes was 67 ms (Figure 1b). The specific SOA was chosen because of certain constraints (frame rate, obtaining an illusion in the illusion conditions) and, above all, similarity with earlier studies of an audio-visual illusion (Shams et al., 2000; Shams, Ma, & Beierholm, 2005).

Setup

Observers sat in a dark cubicle with no ambient light source except the display screen at a viewing distance of 57 cm from the computer screen (Viewsonic 22″ CRT, Professional Series P220f, refresh rate = 80 Hz). The participant's head was stabilized by a chin rest (UHCO Tech Headspot). Software was programmed and presented using MATLAB (Mathworks, Natick, MA, USA) and the Psychophysics toolbox extensions (Brainard, 1997; Pelli, 1997) using a Windows PC system. To ensure that the system was not producing artificial double flashes due to unforeseen problems with synchronizations, delays, etc., a 30-trial simulation was performed in which the peripheral inducer location was covered by a black cardboard piece; only the central target flash was thus visible and its number was duly noted: It always flashed once.

Task

Throughout each trial, there was a constant fixation point at the top of the screen. The observer's task was to judge the number of central target flashes (s)he perceived. Each experiment consisted of 20 trials of each condition, amounting to a total of 100 (= 5 × 20) trials, ordered randomly. The perceived number of target flashes was reported by a corresponding key press on a standard computer keyboard.

Analysis

For each observer and condition, we calculated the mean number of target flashes perceived. One-way repeated measures ANOVA was conducted with number of inducer flashes (0–4) as the main factor and the mean number of target flashes perceived by each subject as the dependent variable. For further analysis, four planned pairwise contrasts were examined, namely, a simple contrast between the zero inducer flash (baseline reference condition), on the one hand, and each of the other non-zero inducer flash conditions, on the other.

Results and discussion

The presentation of inducer flashes caused a clear change in the number of target flashes perceived, with effect size increasing as the number of inducer flashes increased. Figure 2 (red solid lines and filled circles) plots the mean number of central target flashes perceived when 0–4 inducer flashes were presented in the periphery. A one-way repeated measures ANOVA on the number of perceived target flashes after Greenhouse–Geisser correction revealed a significant main effect of number of inducers ($F(1.65, 14.83) = 26.668$, $MS_e = 0.172$, $p \ll 0.0001$). Table 1 shows the summary data demonstrating the effect.

To dissect this effect further, planned contrasts were performed to examine the effect of the presence of inducer flashes on the number of target flash(es) perceived. The zero inducer flash condition constitutes the baseline, against which each of the non-zero inducer flash conditions was compared for long-distance spatial interaction. As can be seen in Figure 2, observers most often correctly reported perceiving one central target flash when no inducer flashes were present and overestimated the number by 16–17% when there was a single inducer present. In contrast, observers reported seeing many more central target flashes when 2, 3, or 4 peripheral inducer flashes were presented, by 47%, 100%, and 105%, respectively. There was no significant difference in the number of perceived central flashes between the baseline
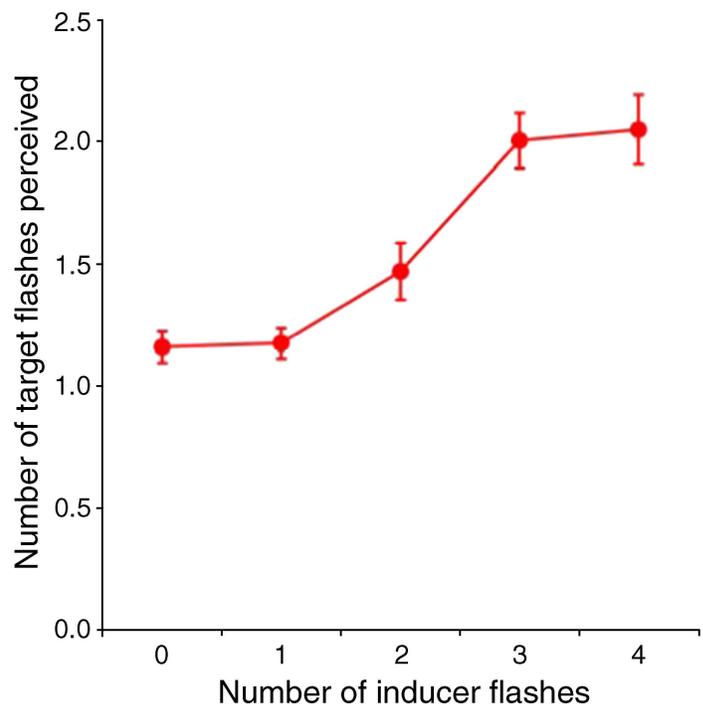

Figure 2. Basic demonstration of phantom flash effect: Counting the number of perceived target flashes. The graph plots the mean (filled red circle) ± *SEM* (red error bars) number of central target flashes perceived (ordinate) as a function of the number of inducer flashes in the periphery (abscissa). Though there was in actuality only one target flash, subjects perceived significantly more flashes when multiple inducers were presented in the periphery.

Number of inducer flashes	Mean number of target flashes perceived	Standard error
0	1.160	0.065
1	1.175	0.062
2	1.470	0.116
3	2.005	0.114
4	2.050	0.143

Table 1. The basic phantom flash effect (Experiment 1).

zero flash condition and the one peripheral inducer flash condition. Planned contrasts between the baseline zero inducer versus each of the non-zero inducer flash conditions confirmed this observation (0 vs. 2 inducers, $p = 0.028$; 0 vs. 3 inducers, $p = 0.0002$; 0 vs. 4 inducers, $p = 0.001$). In sum, two, three, or four inducer flashes around the time of a single target flash led one to perceive additional "phantom" target flashes in the central visual region.

Experiment 2: Target–inducer distance and distance of target from fovea

In the first experiment, the target was close to fixation but in the periphery nonetheless. Temporal vision is more ambiguous in the periphery than at the center of the fovea (McKee & Taylor, 1984). The previous studies of flicker detection had shown various effects of target and distractor position, but it is difficult to separate out contributing factors in the different experiments (Leonards & Singer, 1997; Wilson, 1987; Wilson & Singer, 1981). In Experiment 2, we titrated the effects of target–inducer distance and the eccentricity of the target.

Methods

Observers

Seven, four, and three observers participated in Experiments 2a, 2b, and 2c, respectively. No authors participated.

Stimuli and procedure

In Experiment 2a, the target disk was at an eccentricity of 2° below the fixation point, as opposed to 4° in the previous experiments. The inducer remained at 9°. In Experiment 2b, the target disk was at fixation, and the inducer disk was at an eccentricity of 7° below the fixation.

In Experiment 2c, the target was at fixation and the inducer at 3° below fixation.

Setup

The setup was the same as in Experiment 1.

Task

The task was identical to that in Experiment 1.

Analysis

The analysis was the same as in Experiment 1.

Results and discussion

In Experiment 2a, there remained a modest albeit significant effect of the number of inducer flashes on the perceived number of target flashes ($F(1.41, 8.49) = 6.792$, $MS_e = 0.309$, $p = 0.023$, Greenhouse–Geisser corrected). Figure 3 (green line) plots the mean number of flashes reported. Baseline data from Experiment 1 is also plotted
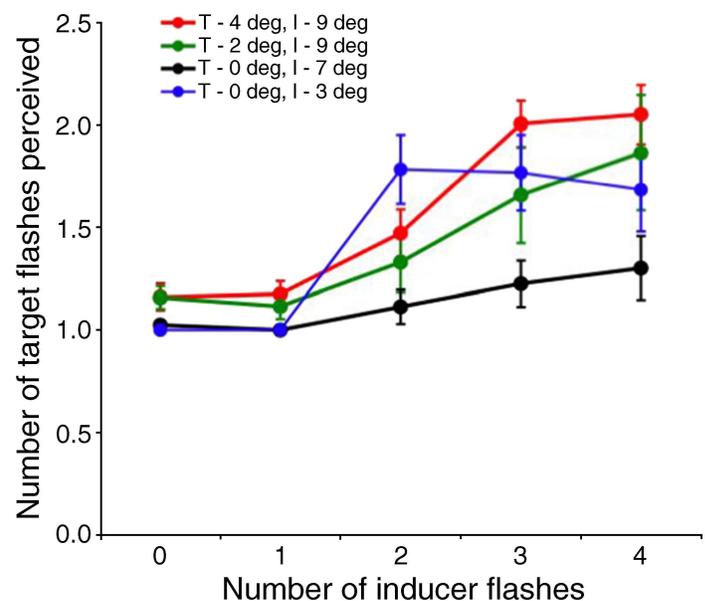

Figure 3. Perceived number of target flashes in 3 separate conditions—foveal distance of target is changed and one condition, the foveal distance of inducer is also changed. In figure legend: T = Target, I = Inducer, and the number beside them indicates eccentricity in degrees. The graph plots the mean ± *SEM* perceived number of target flashes as a function of the number of inducer flashes in the periphery. Data from Experiment 1 are replotted here for comparison (red). Both target–inducer distance and target–fovea distance modulate the effect.

for reference (red line). In comparison to baseline, the perceived number of target flashes was significantly greater when 3 or 4, but not 1 or 2, inducer flashes occurred (0 vs. 3 inducers, $p = 0.047$, 0 vs. 4 inducers, $p = 0.034$, but 0 vs. 1 inducer, $p = 0.356$, and 0 vs. 2 inducers, $p = 0.165$). The results indicate that the phantom flash effect remained, albeit at reduced strength, when the target was positioned closer to the center of gaze.

Follow-up

From Experiment 2a, it was observed that when the target was brought closer to the fovea and the target–inducer separation increased at the same time, the effect was preserved, albeit weakened. We asked whether it was the more foveal placement of the target that weakened the effect or the increased target–inducer separation that caused the weakening. If it is the former, then bringing the target to the fovea while keeping the target–inducer separation the same as Experiment 2a would cause further weakening of the effect. As a follow-up to results obtained in Experiment 2a, Experiment 2b was done with subjects being instructed to foveate directly on the target disk. The rest of the stimuli, procedure, setup, and task remained as in Experiment 2a. Figure 3 (black line) plots the mean number of flashes reported in this condition. One-way repeated measures ANOVA (Greenhouse–Geisser corrected) revealed that the main effect of the modulation of the number of target flashes perceived by inducer flashes was not significant ($F(1.20, 3.61) = 3.488$, $MS_e = 0.063$, $p = 0.144$). Planned contrasts between the baseline zero inducer flash condition and the other conditions found that the perceived number of target flashes was never significantly greater in comparison to the perceived number of target flashes on the baseline condition. (For zero vs. single inducer flash, $p = 0.182$, zero vs. two inducer flashes, $p = 0.310$, zero vs. three inducer flashes, $p = 0.145$, zero vs. four inducer flashes, $p = 0.160$).

The results indicate that when the target is directly fixated (and target–inducer distance kept the same as before), the phantom flash effect is weakened to the point of statistical insignificance. However, it must be mentioned that in post-experimental debriefings, the subjects said that in a very small minority of trials, they were confident that their perceived number of target flashes was more than one. The above comparison isolates the role of target position as a factor in effect size.

Previous studies have indicated a role for target–inducer separation (Wilson & Singer, 1981). If both target eccentricity and target–inducer separation influences the magnitude of the phantom flash effect, then the effect may be recoverable even with a foveal target if the target–inducer separation is sufficiently reduced. Hence, as a further follow-up, Experiment 2c was performed—the target was again at fixation and the inducer was at a reduced separation of 3° below fixation. Figure 3 (blue line) plots the mean number of flashes reported in this condition.

One-way repeated measures ANOVA (Greenhouse–Geisser corrected) revealed that the main effect of the modulation of the number of target flashes perceived by inducer flashes almost reached significance ($F(1.05, 2.09) = 15.62$, $MS_e = 0.123$, $p = 0.054$) after. This indicated some effect of target–inducer separation in salvaging the phantom flash effect. In sum, as expected, targets become more resistant to perturbation as they move toward the fovea and more vulnerable to perturbation as target–inducer distance decreases. Setting these two factors in extreme opposition, we found signs that a directly foveated target could be affected by a nearby inducer.

Experiment 3: Multiple targets, single inducer—Phantom continuity?

The cross-modal double-flash effect has been found to be symmetric (Shams et al., 2005). That is to say, the number of flashes perceived can be increased or decreased, depending on whether the number of beeps is higher or lower than the number of flashes. We look for a similar effect here. If the inducer flashes a fewer number of times than the target, does one perceive fewer target flashes than were actually present?

Methods

Observers

Four observers, two of whom were participants in Experiment 1, participated. None of the authors participated.

Stimuli and procedure

Experiment 3 consisted of two blocks. On trials of the first block, the target flashed between zero and four times and the inducer flashed exactly once. Other stimulus parameters were identical to those in Experiment 1. On trials of the second block, the target flashed between zero and four times, and there was no inducer flash at all.

Setup

The setup was the same as in Experiment 1.

Task

The task was identical to that in Experiment 1. On a given trial, the observer had to count the number of target flashes. Since the second block had no inducer flashes, trials with zero target flashes did not contain any visual

events at all. Observers were instructed to respond zero indicating no target if no flash appeared within 5 s following the preceding trial.

Analysis

For each observer and condition, we calculated the mean number of target flashes perceived. A two-way repeated measures ANOVA was conducted with number of actual targets (0–4) and presence of one inducer versus the absence of inducers as factors.

Results and discussion

The perceived number of target flashes increased in clear accord with the actual number of target flashes in both blocks (Figure 4). Not surprisingly, a two-way repeated measures ANOVA revealed a significant main effect of the actual number of target flashes on the mean number of target flashes perceived ($F(4, 12) = 324.92$, $MS_e = 0.046$, $p \ll 0.0001$). Of importance to the present purpose, the effect of zero versus one inducer was not significant ($F(1, 3) = 0.170$, $MS_e = 0.162$, $p = 0.708$),
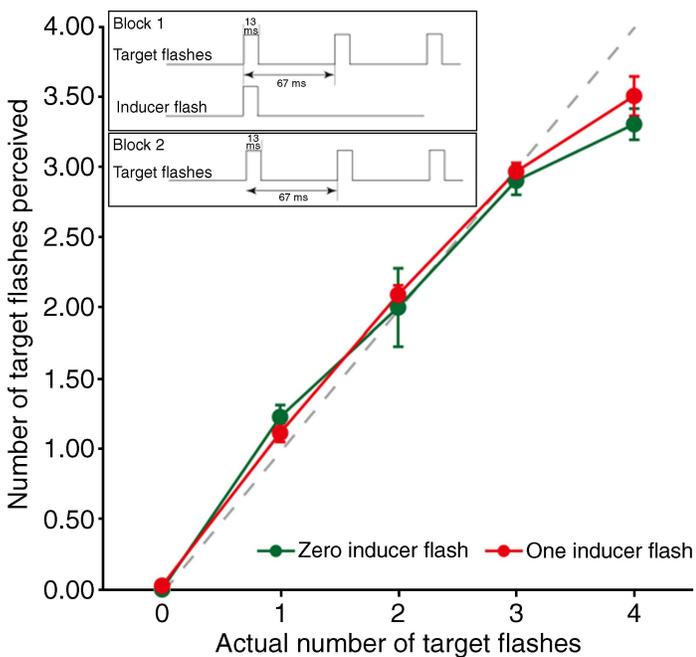

Figure 4. Asymmetry of the phantom flash effect: Perceived number of target flashes, when the actual number of target flashes is varied (0–4) in 2 separate conditions—with zero inducer flashes and one inducer flash. Inset: The temporal profile of the stimuli in the conditions (0 inducer/1 inducer with 0–4 targets). The graph plots the mean ± *SEM* number of target flashes perceived in the zero inducer condition (green) and the one inducer condition (red) as a function of the actual number of target flashes. Subject reports showed high accuracy and no effect of inducer presentation.

and the interaction between the two factors—number of target flashes and number of inducers—was not significant ($F(4, 12) = 0.644$, $p = 0.642$) either. None of the four planned contrasts corresponding to the different numbers of target flashes (1–4) between the zero and one inducer conditions was significant ($p \gg 0.1$; see also Figure 4). That is to say, the perceived number of target flashes was not reduced by the presence of a single versus no inducer. What is more, the mean perceived number of targets was, if anything, slightly higher in the one inducer flash condition than in the zero inducer condition, although the difference was not significant. This indicates that inducer flashes can increase the perceived number of target flashes, but they cannot decrease them. This is in contrast to the symmetry of the cross-modal version of the illusion, where auditory inducers can both increase and decrease the number of visual flashes perceived.

Furthermore, the results indicate that the basic task of counting flashes is not difficult given the position and temporal frequency at which we present our targets. This is in contrast to the flicker detection tasks of the previous studies, where the settings were chosen to be moderately difficult even under baseline conditions (Wilson & Singer, 1981).

We note that when no inducer flashes were present, the baseline number of target flashes was slightly overestimated (mean perceived number of targets = 1.22, *SEM* = 0.09).

Experiment 4: Baseline ambiguity

Results from Experiments 1 and 3 suggest that even in the baseline condition in which no inducer flashes were present, subjects slightly overcounted a single target flash. This might indicate that a singleton flash in the visual field in this case was not an unambiguous percept to start with, and all that an additional inducer does is render the percept more ambiguous. In particular, a hard-edged flash is known to generate a response that is biphasic or even triphasic (Manahilov, 1995). If this response profile is a source of the effect, this would also explain why flashes are overcounted but not undercounted. In the present experiment, we tested this account with a stimulus whose response function would be more monophasic—a high spatial frequency Gabor against a mean gray background. If the phantom flash effect in the previous experiments depends on the multiphasic nature of the response function, then the effect should be abolished here.

Methods
Observers

Four observers participated. None of the authors were participants.

Stimuli and procedure

The display was the same as in Experiment 1 except that the background was gray (14.5 cd/m^2) instead of white and the central target and the peripheral inducer were vertically oriented high-frequency Gabor patches (diameter = 1.5°, frequency = 5 cycles per degree). All other stimulus parameters, procedure, and task were the same as in Experiment 1.

Analysis

The analysis was the same as in Experiment 1.

Results and discussion

Figure 5 plots the mean number of target flashes perceived in the presence of 0–4 inducer flashes. As Figure 5 shows, there was a clear effect of inducer flashes on the number of target flashes perceived ($F(4, 12) = 11.705$, $MS_e = 0.132$, $p = 0.0004$). Planned contrasts between the baseline zero inducer flash condition and the non-zero inducer flash conditions showed that the perceived number of target flashes was significantly greater
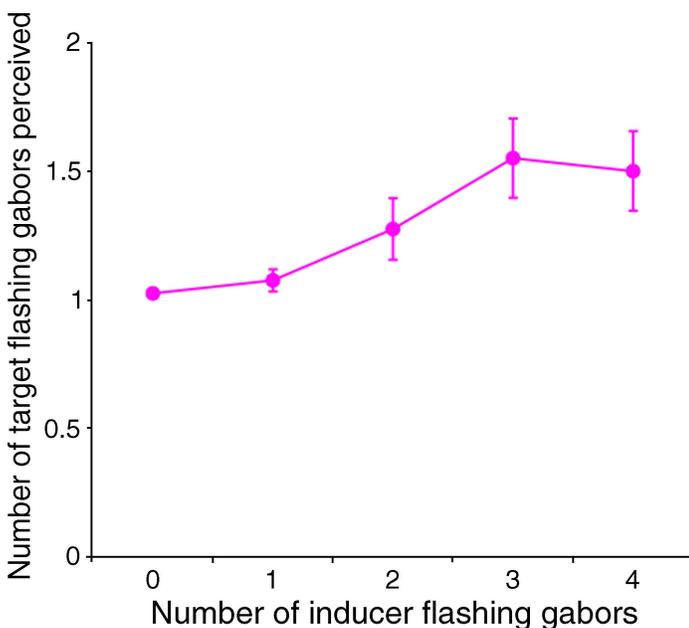

Figure 5. Perceived number of target flashes when the target and inducer are high-frequency Gabor patches on a mean gray background. The graph plots the mean ± *SEM* number of target flashes perceived as a function of the number of inducer flashes. In this condition as well, subjects saw significantly more flashes when multiple inducers were presented. In addition, the slight overcount of single target flash at no inducer flash scenario is mitigated.

when three or four inducers occurred in comparison with none (0 vs. 3 inducers, $p = 0.036$, 0 vs. 4 inducers, $p = 0.047$, 0 vs. 1 inducers, $p = 0.252$, 0 vs. 2 inducers, $p = 0.104$). Overall, the results of Experiment 4 indicate that the phantom flash effect is observable even when target and inducer are vertically oriented high-frequency Gabor patches.

The results show that the effect does not require a target that generates a multiphasic response and is not dependent on high levels of perceptual ambiguity. It bears mention that the mean number of perceived target flashes was 1.025 (*SEM* = 0.14; not significant, as above) when no inducer was present. This amounts to one error per forty trials or half an error per subject. Thus, the baseline ambiguity of the flash in this experiment is negligible, at least at the behavioral level. Other forms of ambiguity at the signal level may still be involved, but the perception of multiple flashes seems to require additional influence from the inducer signals.

Experiment 5: Contextual effects—Collinearity of target and inducer

Context modulates perception through interactions across space between target and context. In other studies of contextual modulation, it has been found that target detection is enhanced when the flanker (inducer) is collinear with the target; the iso-orientation facilitation that results enhances target detection (Polat & Sagi, 1993, 1994a, 1994b, 2007). Here, we examined the effect of collinearity on effect magnitude. If collinearity between target and inducer were to enhance effect magnitude, it would imply that a directed, specific form of spatial interaction underlies the phantom flash effect.

Methods

Observers

Six out of the ten observers in Experiment 1 participated. No authors participated.

Stimuli and procedure

There were two blocks of trials—target and inducer were collinear in the first block and non-collinear in the second block. The white disks of Experiment 1 were replaced by bars (length—1.5°, width—0.5°, i.e., an aspect ratio of 3:1) with the central and peripheral bars at 4° (central) and 9° (peripheral) eccentricities below a fixation point. In the collinear condition, the two bars

were vertical, and in the non-collinear condition, the bars were horizontal.

Setup

The setup was the same as in Experiment 1.

Task

The task was identical to that in Experiment 1, except that in each of the two blocks there were ten trials at each inducer flash condition (0–4), amounting to a total of fifty (= 5 × 10) trials per block, ordered randomly.

Analysis

For each observer and condition, we calculated the mean number of target flashes perceived. A two-way repeated measures ANOVA was conducted with the number of inducers (0–4) and target–inducer alignment (collinear/non-collinear) as main factors. For further analysis, four planned pairwise contrasts were conducted for each block separately, namely, between the zero inducer flash condition (baseline) and the other 1–4 inducer flash conditions.

Results and discussion

The presentation of inducer flashes caused a clear change in the number of target flashes perceived (Figure 6): The two-way repeated measures ANOVA revealed a significant main effect of the number of inducers on the mean number of target flashes perceived ($F(4, 20) = 16.439$, $MS_e = 0.252$, $p \ll 0.0001$), replicating the main effect. With respect to the purposes of this experiment, target–inducer alignment (collinear/non-collinear) did not have a significant effect on perceived number of target flashes ($F(1, 5) = 0.387$, $MS_e = 0.052$, $p = 0.561$). The interaction between the two factors (number of inducers and target–inducer alignment) was not significant either ($F(4, 20) = 1.321$, $p = 0.296$). Planned contrasts between the zero inducer flash baseline and the 1–4 inducer conditions demonstrated that the perceived number of target flashes was significantly greater in comparison to baseline when 2, 3, or 4 rather than when 1 inducer flash occurred in both the collinear and non-collinear conditions ($p < 0.05$ in all cases except 1 inducer flash).

Thus, the effect is robust to variation in stimulus shape (bar in place of disk) and contextual relationship (collinearity/non-collinearity) between target and inducer. Phantom flashes are perceived in both the collinear and non-collinear conditions and to a similar degree. This extends upon the experiments of Wilson and Singer (1981),
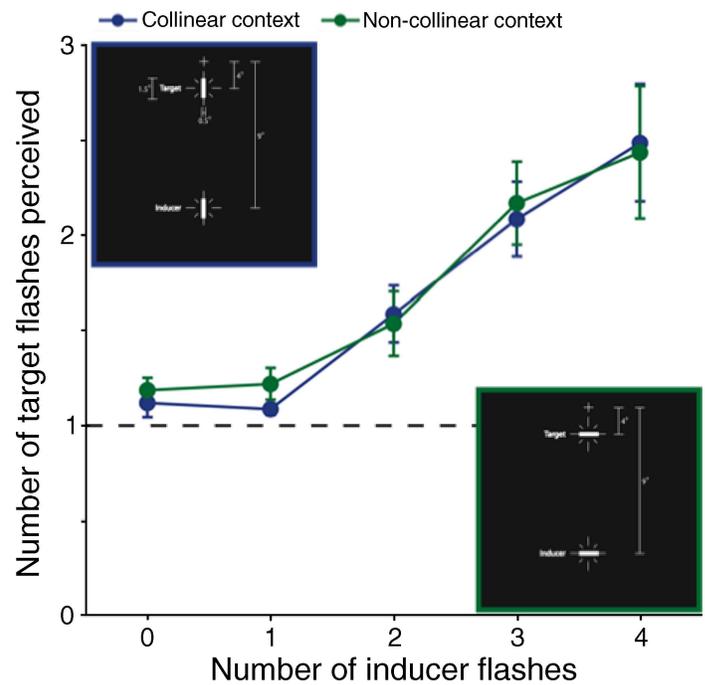

Figure 6. Perceived number of target flashes in 2 separate conditions—when the target and inducer are collinear or non-collinear. Inset: Illustration of the collinear (blue framed) and non-collinear (green-framed) conditions. The graph plots the mean ± *SEM* number of flashes perceived in the collinear condition (blue) and non-collinear condition (green) as a function of the number of inducer flashes. Both conditions showed the main effect of additional perceived flashes. No significant difference was found between the conditions.

who found that the interaction persists when target and inducer have different shapes. These results suggest that the phantom flash effect is not based on directed, specific forms of lateral spatial interaction, such as those found in target detection tasks.

Experiment 6: Opposite polarity of target and inducer

What perceptual mechanisms then account for the phantom flash effect? The simplest possibility is some kind of low-level energy transfer across space. More specifically, an increment (decrement) in inducer luminance could be transmitted via some long-distance spatial mechanism in the brain to a distant, attended location in space and be perceived as a corresponding increment (decrement) in target luminance. This would imply that if target and inducer are of opposite polarity, the phantom flash effect would be eliminated or at least reduced considerably.

Methods

Observers

Observers were six naive volunteers who participated in Experiment 1. No authors participated.

Stimuli and procedure

The display was the same as in Experiment 1 except that the background was gray (14.5 cd/m^2) instead of white, and the central target was black (0.05 cd/m^2) instead of white and was of opposite polarity from that of the peripheral inducer (76.6 cd/m^2). All other stimulus parameters, procedure, and task were the same as in Experiment 1.

Analysis

The analysis was the same as in Experiment 1.

Results and discussion

Figure 7 plots the mean number of target flashes perceived in the presence of 0–4 inducer flashes. As
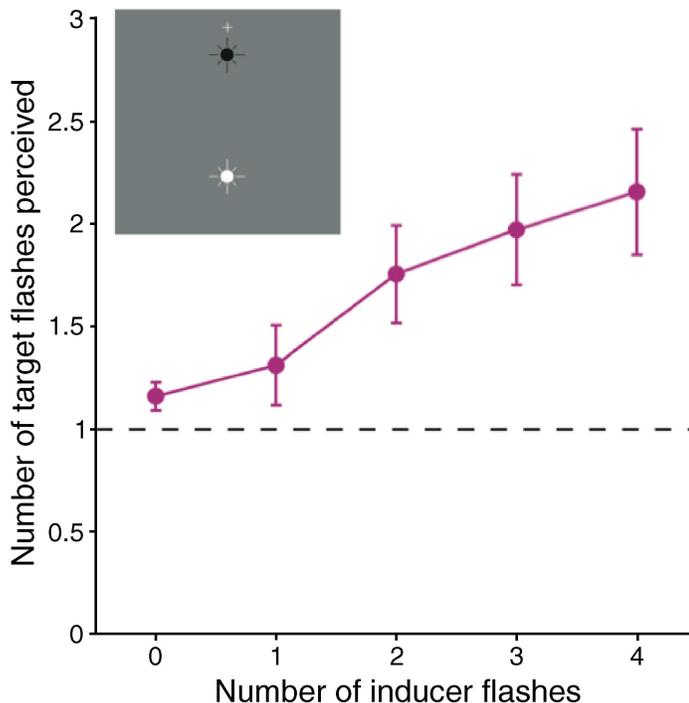

Figure 7. Perceived number of target flashes when the target and inducer are of opposite polarity. Inset: Illustration of the opposite polarity condition—black target, white inducer, gray background. The graph plots the mean ± *SEM* number of target flashes perceived as a function of the number of inducer flashes. In this condition as well, subjects saw significantly more flashes when multiple inducers were presented in the periphery.

Figure 7 shows, there was a clear effect of inducer flashes on the number of target flashes perceived ($F(4, 20) = 8.140$, $MS_e = 0.132$, $p = 0.0005$). Planned contrasts between the baseline zero inducer flash condition and the non-zero inducer flash conditions showed that the perceived number of target flashes was significantly greater when three or four inducers occurred in comparison with none (0 vs. 3 inducers, $p = 0.048$, 0 vs. 4 inducers, $p = 0.038$, 0 vs. 1 inducers, $p = 0.523$, 0 vs. 2 inducers, $p = 0.077$). Overall, the results of Experiment 6 indicate that the phantom flash effect is observable even when target and inducer are of opposite polarity, which argues against low-level energy transfer as a complete account of the phantom flash effect. This is in line with similar results with the original flicker detection task (Leonards & Singer, 1997).

This also has implications for the neural pathways involved in the inducer–target interaction. Classical studies have demonstrated that the ON and OFF cells, the cells that exclusively respond to light increment and decrement, respectively, remain segregated in the retina and the visual thalamus but not at the level of primary visual cortex and beyond (Schiller & Malpeli, 1978). Were these segregated ON and OFF pathways responsible for the phantom flash effect, having targets and inducers of opposite polarity would eliminate the effect. This was not the case, suggesting that cortical pathways, rather than subcortical structures, are at least partly responsible for the effect. The robust effect across targets and inducers of opposite polarity indicates interactions between ON and OFF signals. This argues against a mechanism based on lateral signaling in the subcortical portion of the geniculostriate pathway.

Experiment 7: Dichoptic presentation

Signals from both eyes converge at the level of the visual cortex. Thus, if the target and inducer are presented to two different eyes (dichoptic presentation) and if the phantom flash effect is found to persist, this would indicate that the effect occurs downstream of binocular convergence, i.e., the effect has a cortical locus. The prediction was tested in the next experiment.

Methods

Observers

Four naive observers participated.

Stimuli and procedure

The display was the same as in Experiment 1 except that the central target and the peripheral inducer were

presented dichoptically using a mirror stereoscope. Outside the target and inducer, there was a rectangular, thin, high-contrast, oriented border in order to rapidly help bring the two eyes into alignment. The target was presented to one eye and the inducer to the other. Observers sat comfortably in a chair and viewed the monitor through a careful arrangement of mirrors adjusted individually for each observer so that the one disk on the screen projected exclusively to the left eye and the other disk to the right. The target and inducer presentation was randomized between the two eyes. All other stimulus parameters, procedure, and task were the same as in Experiment 1.

Analysis

The analysis was the same as in Experiment 1.

Results and discussion

Figure 8 plots the mean number of target flashes perceived in the presence of 0–4 inducer flashes. As Figure 8 shows, there was a clear effect of inducer flashes on the number of target flashes perceived ($F(4, 12) = 8.181$, $p = 0.002$). Planned contrasts between the baseline zero inducer flash condition and the non-zero inducer flash conditions showed that the perceived number of target flashes was significantly greater when three or four inducers occurred in comparison with none (0 vs. 3 inducers,
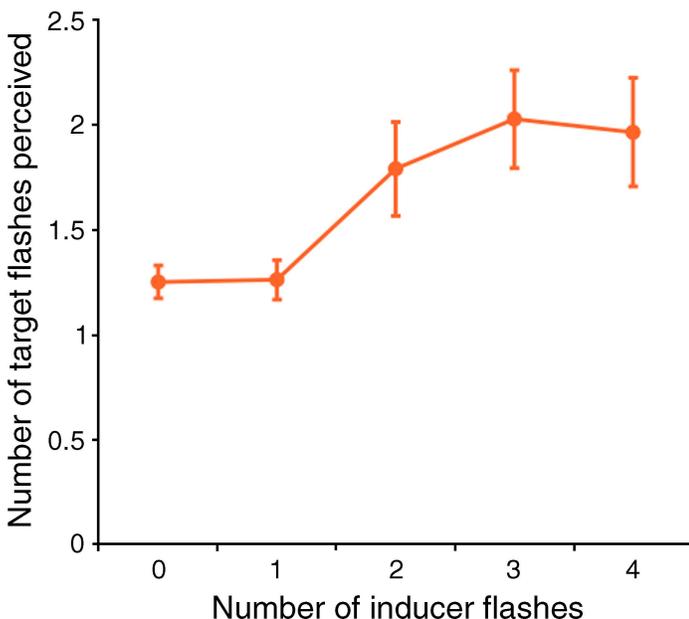

Figure 8. Perceived number of target flashes when the target and inducer are presented dichoptically. The graph plots the mean ± *SEM* number of target flashes perceived as a function of the number of inducer flashes. In this condition as well, subjects saw significantly more flashes when multiple inducers were presented.

$p = 0.023$, 0 vs. 4 inducers, $p = 0.049$, 0 vs. 1 inducers, $p = 0.886$, 0 vs. 2 inducers, $p = 0.062$). Overall, the results of Experiment 8 indicate that the phantom flash effect is observable even when target and inducer are presented dichoptically. The results are consistent with the results from the flicker detection task used in Leonards and Singer (1997). This indicates that monocular interactions are not sufficient to explain the phantom flash effect.

Experiment 8: Target and inducer in different hemifields

In experiments thus far, the target and inducer(s) were displayed in the same visual hemifield. We asked if the phantom flash effect is diminished or extinguished when target and inducer are placed in different (upper and lower) hemifields. Because the anatomical maps of space are continuous across this divide in areas such as V1 but physically separated in areas such as V2 and V3, the pattern of effect strength across the hemifield line could be informative as to possible sites of interaction underlying the effect.

Methods
Observers

Observers were eight volunteers who participated in previous experiments. No authors were among the participants.

Stimuli, procedure, and task

The display consisted of two white disks flashing on a black background, each subtending 1.5° of the visual field. One of the disks (the target) was at 4° eccentricity above the fixation point and the other disk (inducer) was at 5° eccentricity below the fixation point. All other parameters of stimuli and procedure were the same as Experiment 1. The task was the same as in Experiment 1—count the number of target flashes on each trial.

Analysis

The analysis was the same as in Experiment 1.

Results and discussion

As Figure 9 shows, there continued to be a strong effect of inducer flashes on the number of target flashes perceived ($F(1.53, 10.70) = 18.279$, $MS_e = 0.062$, $p = 0.0006$,
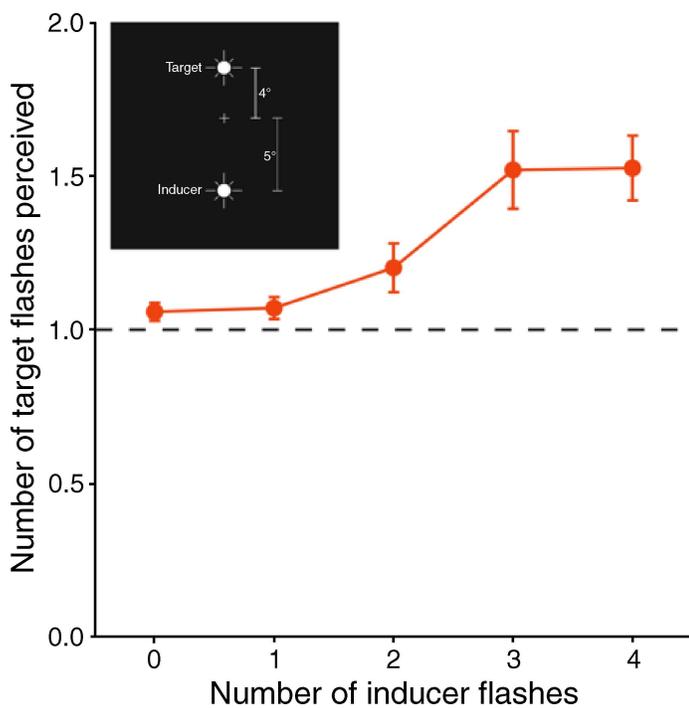
Figure 9. Perceived number of target flashes when the target and inducer are in different hemifields. Inset: Illustration of the different hemifield condition—Target in upper hemifield and inducer in lower hemifield. The graph plots the mean ± SEM number of target flashes perceived as a function of the number of inducer flashes. In this condition as well, subjects saw significantly more flashes when multiple inducers were presented.

Greenhouse–Geisser corrected). Planned contrasts between the baseline zero inducer flash condition and each of the 1–4 inducer flash conditions showed that the perceived number of target flashes was significantly greater when 2, 3, or 4 inducer flashes occurred in the periphery (0 vs. 2 inducers, $p = 0.034$, 0 vs. 3 inducers, $p = 0.004$, 0 vs. 4 inducers, $p = 0.001$ but 0 vs. 1 inducer, $p = 0.516$). These results were remarkably in accord with those of Experiment 1. The results indicate that the phantom flash effect is robust and remains even when the target and inducer are in different visual hemifields. The finding thus suggests that the effect is not based on lateral propagation of signals in visual areas such as V2 and V3, where anatomical maps for each hemifield are segregated.

General discussion

Here, we paired a variable number of inducer flashes in one location of the visual field with a single target flash in another location of the visual field. The presence of inducers caused one to perceive phantom flashes in the target location. Specifically, a significantly greater number of target flashes were reported when a target flashed once and was accompanied by two, three, or four as compared to zero inducer flashes in the periphery. We call this the phantom flash effect. The phantom flash effect was robust across many conditions—the effect was replicated when target and inducer(s) were of opposite polarity, in different hemifields, or if they were non-collinear. Modulation of the effect was found based on target proximity to the fovea and the size of target–inducer separation. Thus, across a range of experimental settings, the number of target flashes reported was greater than the number of target flashes that actually occurred but only in the presence of multiple inducers.

Comparison with the original flicker detection studies

In the main, we replicate and extend on the findings of Leonards and Singer (1997), Wilson (1987), and Wilson and Singer (1981). However, a number of differences in our methodology and results should be noted.

The earlier studies intermixed trials with one or two target flashes and derived results based on subject error rates in a two-alternative forced-choice reporting task. In addition, the stimulus settings had been chosen to be of "moderate difficulty." In both Wilson (1987) and Wilson and Singer (1981), three subjects had to be rejected for failing to reach criterion performance levels when the target was presented without any inducers present. This suggests that target perception in past studies was somewhat ambiguous even at baseline.

In contrast, the target always flashed once on all the experiments in the present study, and our observers were given no prompting as to the distribution of stimulus conditions. Observers were free to report any number of flashes they perceived in a given trial. Further, the stimulus settings posed little difficulty for task performance—observers performed nearly perfectly in counting the number of flashes in conditions without inducers (Experiment 6).

In terms of results, the largest discrepancy with the earlier studies was that we did not find an effect in the reverse direction, namely, where the presence of inducers caused the perceived number of target flashes to be smaller than the actual number of target flashes. One possible reason for this may be the differences in trial and reporting structure. When total error is taken to be a measure of effect size, 2AFC paradigms are susceptible to observer bias (Green & Swets, 1966) due to a "regression to the mean." Alternatively, the level of task difficulty imposed by the stimuli may account for the difference. In any case, the earlier studies did not focus on the internal symmetry of the effect. In general, they reported only total error rates, and where the directions of errors were broken down, results were somewhat inconsistent in magnitude (Wilson, 1987; Wilson & Singer, 1981).

Influence of context on perception

More broadly, our findings descend from a rich literature demonstrating the varied influence of center–surround interaction on perception (e.g., Blakeslee & McCourt, 2008; De Valois, Webster, De Valois, & Lingelbach, 1986; Ebbinghaus, 1902; Müller-Lyer, 1889; Polat & Sagi, 1993; Ratliff, 1965; Wenderoth & Johnstone, 1988). Within this context, some particular aspects of our methodology and the resulting phenomenology are of note.

Typically, the presence of a surround stimulus affects the perception of some feature of a present and visible target such as its location, color, luminance, or orientation; here, the inducer caused the observer to perceive additional targets, when, in fact, they did not occur. In most other past studies (but see Polat & Sagi, 1993, 1994 for exceptions), the surround stimulus is physically adjacent to the target and envelopes it and is therefore both more foveal and peripheral to it. Here, the target and inducer were located at a moderate distance from each other and did not abut.

The spatial spread of contextual effects is often characterized by a pattern of collinear facilitation (Polat & Sagi, 1993, 1994a, 1994b). In experiments involving target detection, clear improvement in performance has been observed with relatively large spatial separations between the target and inducer, especially when they are placed collinearly. In our study, no change was observed in the magnitude of the effect in the present set of experiments if the target and flanker were aligned along their major axis (collinear condition) compared to a condition where the target and flanker were not aligned along their major axis (non-collinear condition). This suggests that the mechanism for the phantom flash effect is somewhat different from the classical flanker facilitation paradigm.

Finally, studies of contextual effects generally use stimuli lasting for seconds, as opposed to the present study in which all flashes lasted for 13 ms. Studies of visual masking in which the stimuli are of similarly brief duration as in the present study have shown dramatic effects of center–surround interaction on target detectability (Breitmeyer et al., 2006) but in exactly the opposite direction—the stronger effect of the mask induces invisibility of the target rather than phantom visibility, as observed here. It should be noted that a single transient can cause subjective contrast enhancement for a second transient after the initial transient that is temporally separated from the initial transient, the best enhancements being at an SOA of 110 ms (Bachmann, 1988). However, for about 40 ms, forward masking reigns. In the present set of experiments, there was no physical presence of a second transient to be perturbed. Even allowing for an "unclean" perception for a single transient, the physical flash itself, by dint of being a single physical transient, does not have the kind of SOAs required to mimic the mechanisms reported in the enhancement of subjective contrast reported in the earlier study

(Bachmann, 1988), which is important in understanding the difference in finding.

Baseline ambiguity

The stimuli used in our experiments demonstrating the basic effect were sharp-edged. Previous studies have shown that the impulse response function to the transient presentation of sharp-edged stimuli is bi- or triphasic (Ikeda, 1986; Stork & Falk, 1987). It seemed possible that the multiphasic nature of the response could be the reason underlying the overestimation of numerosity. In Experiment 4, we used stimuli without hard edges so as to give rise to monophasic impulse responses. The results confirmed that we had reduced target ambiguity enough so that a single target without inducers was almost never overcounted. Under these conditions, we still found a phantom flash effect, with a small degree of reduction in strength. This indicates that the multiphasic response function in our basic stimuli may have contributed to part of the effect, but that the effect survives even when signal ambiguity is minimized.

Eye movements

Sensory-perceptual effects are strongly modifiable by eye movements (for example, fluctuations in sensitivity, eye movement-related attentional effects, etc.). One may argue that due to eye movements, the eyes move from fixation to the locus of the inducer flashes. However, from Experiment 1, in case of 2 and 3 inducer flashes, where the phantom flash effect is quite pronounced, the total duration of the inducer flash train and interflash interval is 147 ms (in case of 3 inducer flashes) and 80 ms (in case of 2 inducer flashes; Figure 1), hardly enough for a saccade to happen and fixate on the inducer locus, which is in the order of 150–200 ms (Fischer & Ramsperger, 1984). While the inducer flash train is always present at the periphery as the subjects fixates on the fixation spot, an eye movement to the inducer flash train locus does not explain the phantom flash effect. The presence of the inducer and target flashes explicitly in the different hemifields condition makes it harder to argue that the percept of the target percept is due to eye movement to the inducer, which was in a different vertical hemifield than the target.

Post-perceptual interactions with transient targets

The brief nature of the target has another implication for the contextual interaction, since additional inducer flashes occur after the target flash has already been extinguished

(see temporal profile in Figure 1). The interaction can be described as post-sensory, in the sense that the additional target flashes must interact with residual visual signals that remain after target offset, over SOAs as high as 335 ms. The terms "sensory" and "post-sensory" are defined in terms of the timing of the stimulus with respect to perceptual decision. Post-sensory is when the perceptual decision about some property of the stimulus is made after the stimulus is no longer present in the physical world and afferent signals signaling the presence of the stimulus have been extinguished or are decaying rapidly.

Thus, this study indirectly extends earlier work that has demonstrated differences between sensory and post-sensory processing and perception and the influence of context and attention on each (Sheth & Shimojo, 2000, 2001). The neural representation of a stimulus that is current on the retina is different from the representation of a stimulus that is extinguished. For instance, the presence of a moving surround during the time period that a high-contrast target remains on leads to a bias in judgments of target location in a direction *opposite* the inducer. However, the presence of that moving surround during the time period after the target's offset biases judgements in the *same* direction as the inducer (Sheth & Shimojo, 2003). This pattern parallels the effect of signal strength upon the classical illusion of induced motion, whereby stationary targets appear to be in motion if they are embedded in a moving surround. It has been found that targets of high strength appear to move *opposite* the inducer, but targets of lower strength appear to move *with* the inducer (Murakami & Shimojo, 1993). Thus, it appears that the relationship between sensory and post-sensory targets is similar to the relationship between strong and weak targets.

This variability in effect is even more pronounced when the target is transient. Since a new percept needs time to form, the percept is not fully crystallized during the brief life span of a flashed stimulus, leading to a weak representation. This ill-formed percept of a target is affected by surround stimuli presented both during and after the target (Sheth & Shimojo, 2000; Zivotofsky, White, Das, & Leigh, 1998).

It is likely that both the post-sensory nature of the interaction and the transient nature of the target contribute to the phantom flash effect. Contextual effects are often found to reverse with changes in target strength, with suppressive effects on strong targets becoming facilitative effects on weak targets (Somers et al., 1998; Stemmler et al., 1995). The detectability of a signal at threshold is dependent on a probability summation over time and space rather than a peak response criterion (Georgeson, 1987; Watson, 1979; Wilson, 1980). Conceivably, in the present case, after the extinguishing of the physical target flash, the neural signal persists in the peri-threshold zone, for a small time window, enough for temporal and spatial summation, effected through modulation by the inducer flashes.

Unidirectionality of the effect—Relationship to the audio-visual flash illusion

The phantom flash effect was found here to be unidirectional. The number of target flashes perceived can be elevated by the presence of multiple inducers, but there is no corresponding reduction in perceived target flashes when a single inducer accompanies multiple targets. The unidirectionality argues against an explanation based on simple cue integration, a framework often used to explain the audio-visual flash illusion that inspired this study. It is interesting to note that two flashes accompanied by a single beep is typically perceived as a single flash (Shams et al., 2005). Had a similar effect been found here- multiple target flashes accompanied by a single inducer flash being perceived as a single target flash—one could argue for a simple integration of information from the two locations. Because this was not the case, the two locations do not appear to be combined in a straightforward, linear way.

Furthermore, the cross-modal interaction is found mainly in situations with small discrepancies between the two inputs, e.g., when the numbers of flashes and beeps differ by one (Shams et al., 2005). Here, in contrast, a location in visual space affected the perception of flashes in another location even when the numbers of flashes between the two locations differed by more than one, e.g., the illusion was no weaker when there were three inducer flashes in the periphery compared with two and was in fact stronger. Thus, the interaction between the two visual locations cannot be seen as a form of partial integration. Indeed, the differences between the phantom flash illusion and the audio-visual flash illusion (Shams et al., 2000) suggest that the broad similarities between the two phenomena may be quite superficial. It is possible that the underlying mechanisms in the two cases are quite different, but in a case of functional convergence, they give rise to remarkably similar phenomena.

When applying Bayes' theory to the audio-visual flash illusion (Shams et al., 2005), signals from the two modalities are assumed to be independent. However, this assumption does not directly carry over into visual–visual interactions. From early studies (Ebbinghaus, 1902; Müller-Lyer, 1889; Zöllner, 1860), we know that neural signals in different parts of the visual map are not mutually independent. Thus, whether or not the mechanism in the visual–visual case is the same as that for the audio-visual case, a model that attempts to unify both illusions must take into account the issue of varying cue independence.

Physiological models and anatomical locus

As mentioned earlier, the phantom flash effect is likely due to contextual modulation of post-sensory signals that

outlast the offset target flash. In our experiments, a flash at the target location provides direct input to the retinotopically corresponding target neuron(s), and neurons responding to the inducer flashes provide additional contextual input to the target neurons. From a physiological perspective, the presence of a target in a location in space causes a neuron with the retinotopically corresponding receptive field to raise its membrane potential to the firing threshold. This process is known to render a neuron highly sensitive to synaptic (and other) noise (Schneidman, Freedman, & Segev, 1998; Strassberg & Defelice, 1993). When a neuron is in such a state, input from other sources can modulate its activity enough to affect the perceptual outcome. This is in line with our experimental finding: Inducers paired with a single target flash lead the observer to report additional target flash(es), but this is much less likely when no target flash occurs at all. We propose that the physical flash at the target location places the target neuron in the unstable regime allowing a stream of visual transients from the inducers to yield a series of spike bursts in the target neurons. These additional fluctuations in the target signal lead to the perception of additional flashes.

Such a mechanism based on signal transients would explain why the perceptual effect failed to fit the expectations of a cue integration scheme. Cue integration predicts both increase and decrease in target count depending on the relative numbers of target and inducer flashes, whereas the signal transients predict only increase. Input from inducers can add more fluctuations to the target signal, but the absence of extra inducers simply leaves the target signal intact. Furthermore, cue integration predicts maximal effect when inducers and targets are similar. With a signal transient mechanism, this is not a requirement. The effect size simply increases as the number of inducer flashes increases, even if target and inducer are dissimilar. In both senses, the signal transient model is better aligned with our results.

A question that remains is how the signal propagates from the neurons that respond to the inducer location to influence the neurons that respond to the target location. A number of known lateral, feedforward and feedback mechanisms are considered here. Retinal ganglion cells show facilitatory modulation of response in a part of the visual field by a spot of light in a different part of the visual field. In the periphery effect (McIlwain, 1966) and the shift effect (Fischer & Krueger, 1984; Krueger, Fischer, & Barth, 1975), retinal ganglion cells change their firing rate in response to moving patterns far outside the classical receptive field of the retinal ganglion cell. However, these effects are unlikely to be related, because we found the phantom flash effect to remain robust when targets and inducers are of opposite contrast polarities. The effect thus seems to involve interactions between on and off signals, and the pathways responding to on and off transients remain anatomically separate until they reach the striate cortex (Schiller, 1982).

Outside of the geniculostrate pathway, other subcortical structures may potentially relay signals from the inducer to the target location. One such structure is the superior colliculus, which is sensitive to transients, and sends afferents to the koniocellular layers of the lateral geniculate nucleus (LGN), as well as to the pulvinar, which in turn projects to various visual association cortices. Previous studies of the phantom flash illusion indicate that the inducer signal is mediated by a luminance-sensitive (alpha/M) pathway (Leonards & Singer, 1997), which is consistent with the response characteristics of the superior colliculus and its ascending inputs (Schiller & Malpeli, 1977; Schiller, Malpeli, & Schein, 1979).

Another subcortical route that may carry a modulatory signal from inducer to target locations is the set of non-specific projections from the thalamus to cortex. Whereas neurons in the LGN are characterized by specific, visuo-spatially organized inputs and outputs, other thalamic neurons project non-specifically to targets throughout the cortex (e.g., intralaminar nucleus, Steriade et al., 1997; thalamic "matrix," Jones, 2001). A number of related theories posit that conscious perception relies on the combination of activity propagating through both types of systems (Bachmann, 1984, 1997; John, 2002; Llinas & Ribary, 1993; Llinas, Ribary, Contreras, & Pedroarena, 1998). In these theories, the wave of activity propagating quickly through the specific pathways of the LGN must be reinforced by a later activity that propagates through the slower non-specific thalamic projections. These theories are complementary to the signal transient model we propose. The LGN pathways would be responsible for the early sensory processing of the target signal, while the non-specific pathways would carry widely spreading activity from the inducers in the post-sensory period.

Mechanisms at the cortical level are likely to be involved as well. Our finding that the phantom flash effect diminishes with increasing distance between target and inducer suggests the involvement of lateral cortical connectivity, as there is neurophysiological data showing that connectivity between two sites in the cortex generally declines with distance (Enroth-Cugell & Robson, 1966; Gilbert, 1983). Visual transients in cells corresponding to one part of visual space could be transmitted via lateral connections to neighboring cells with adjacent receptive fields. Over the course of a few milliseconds, cells with distant receptive fields would come to show a faint visual echo of the initial distant activation, especially if they were already near threshold due to direct stimulation. On the other hand, the lack of orientation tuning in the phantom flash effect is not consistent with other known properties of lateral connectivity in the visual cortex. In general, anatomical connectivity is anisotropic in orientation (Angelucci et al., 2002; Budd & Kisvarday, 2001; Yoshioka, Blasdel, Levitt, & Lund, 1996). Neurophysiological studies of contextual effects have confirmed lateral interactions between sites corresponding to distant locations in space, but these contour integration mechanisms

are orientation-tuned (Gilbert, Ito, Kapadia, & Westheimer, 2000; Ito & Gilbert, 1999). It is possible that such orientation tuning is present in the mechanisms of the phantom flash illusion, but that the test we conducted was not sensitive enough to reveal a small difference in interaction strength.

Finally, it is possible that the post-sensory perturbations may be provided by reentrant processing from higher cortical levels (Di Lollo, Enns, & Rensink, 2000). Visual evoked potential studies are likely to be helpful in the resolution of this question. The phantom flash effect was found to be robust in dichoptic presentation and when inducers and targets were of opposite polarity or opposite orientations. This raises the possibility of an explanation based on higher level event detection, where the low-level spatial identities of the target and the inducer(s) matter less. It is plausible that reentrant processes may be directed back not only at their original feedforward sources but may modulate processes more widely. Thus, activity elicited by the inducers may feed back to target-specific neurons.

Conclusion

Using a target flash counting task in the presence of peripheral inducers, we find that inducers can increase but not decrease the number of flashes seen. This is a distinct departure from the seemingly similar visual effects caused by auditory inducers. This indicates that the Bayesian cue integration model proposed for the cross-modal effects does not apply to this within-modal case. Rather, a signal transient propagation model appears to be a better fit. We find the phantom flash to be robust across a number of target–inducer conditions, narrowing the likely range of neural substrates.

Acknowledgments

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