Effects of luminance and saccadic suppression on perisaccadic spatial distortions

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Visual directions of foveal targets flashed just prior to the onset of a saccade are misperceived as shifted in the direction of the eye movement. We examined the effects of luminance level and temporal interactions on the amplitude of these perisaccadic spatial distortions (PSDs). PSDs were larger for both single and sequentially double-flashed stimuli with low than high luminance levels, and there was a reduction of PSDs for low luminance targets flashed immediately before the saccade. Significant temporal interactions were suggested by PSDs for a pair of sequentially presented flashes (ISI = 50 ms) that could not be predicted from the single-flash distortions: PSD increased for the first flash and decreased for the second compared to the single-flash distortions. We also found that when the flash pair was presented near saccade onset, the perceived distortion of the earlier flash overtook that of the later flash, even though the late flash occurred closer in time to the saccade. To explain these effects, we propose that stimulus-dependent nonlinearities (contrast gain control and saccadic suppression) influence the duration of the temporal impulse response of both single- and double-flashed stimuli.

Keywords: eye movements, perisaccadic, extra-retinal, visual persistence, impulse response function, luminance, saccadic suppression, contrast gain control


Introduction

Perceived directions of objects in the world are usually unaffected by changes in retinal image location that are caused by active changes in eye position (von Helmholtz, 1866). This perceptual stability is achieved in part by summing retinal image locations with extra-retinal estimates of eye position in the orbit to yield visual directions in head-centric coordinates (von Holst, 1954; von Holst & Mittelstaedt, 1950). However, retinal and extra-retinal signals exist on a longer time scale than the brief (25–100 ms) duration of a saccade, and significant distortions of perceived visual direction are reported for visual targets that are briefly flashed near the time of a saccade (Dassonville, Schlag, & Schlag-Rey, 1992; Honda, 1991; Mateeff, 1978; Matin, 1976; Matin & Pearce, 1965). These distortions are characterized by two components: a uniform shift of position coupled with a compression of visual space around the saccade target (Morrone, Ross, & Burr, 1997), which are thought to reflect distinct visual processes (Michels & Lappe, 2004; Ostendorf, Fischer, Finke, & Ploner, 2007). The “compression” component occurs for objects flashed near the saccade target (Kaiser & Lappe, 2004) and is also modulated by the presence of saccadic visual references (Lappe, Awater, & Krekelberg, 2000), although these references are not strictly necessary (Awater & Lappe, 2006). The “shift” component of these perisaccadic spatial distortions (PSDs) is not as sensitive to the presence of visual references and can be isolated by using stimuli flashed near the pre-saccadic fixation point. Because the “shift” component appears to depend on the extra-retinal eye position signal, it is used as a means of studying the process that transforms retinal position signals into head-centric coordinates.

The time course of such PSDs has been studied for both single flashes and pairs of flashes. PSDs can occur for targets flashed as much as 100 ms before and after saccade onset (e.g., Honda, 1991). Earlier flashes (before the saccade onset) are displaced in the direction of the saccade, while later flashes (during/after eye movement) may shift against the eye movement direction. Sogo and Osaka (2002) showed that the perceived relative positions of sequential flash pairs are accounted for, in part, by the retinal slip of flashes presented during the saccade. However, saccade-related retinal slip cannot account for the PSD of targets presented before the saccade.

This paper examines two models that have been proposed to account for the time course of PSDs. The
outflow theory for PSDs begins the efference copy signal earlier than actual eye movement and has it persist slowly throughout and after the saccade (Honda, 1991). The outflow theory is supported by extra-retinal correlates in the superior colliculus and frontal eye fields that can precede the saccadic by 100 ms (Bruce, Goldberg, Bushnell, & Stanton, 1985; Goldberg & Bushnell, 1981; Wurtz & Goldberg, 1972). A more recent “persistence-shift theory” builds on the outflow theory. It computes a position estimate of the flashed target from the weighted average (over time) of the target’s temporal impulse response (TIR) and the extra-retinal eye position signal (Matin, Pola, & Matin, 1972; Pola, 2004, 2007). The persistence-shift model predicts that, ceteris paribus, stimulus factors that influence the persistence of the flashed target should affect the PSD. We performed experiments testing three such hypotheses:

1. increasing persistence of pre-saccadic flashes (i.e., temporal impulse response) should increase PSDs,
2. since saccadic suppression compresses the temporal impulse response (Burr & Morrone, 1996), the amplitude of PSDs should actually decrease right before the onset of a saccade, and
3. interaction between paired flashes should increase with temporal overlap of their TIRs.

While previous studies have examined PSD for stimuli presented over a large range of times to saccade onset (TSOs), we have intentionally restricted our investigation to stimulus conditions in which a flash occurs before the saccade (negative values of TSO). In other words, every spatial distortion we consider has occurred for a target that was physically extinguished before any eye movement began. By limiting ourselves to these pre-saccadic flashes we ensure that the retinal locus stimulated at each TSO is identical and we can presume that any differences in PSD, as a function of TSO, will reflect internal processes (i.e., changes in the TIR). Furthermore, the greatest magnitude of PSD occurs for targets presented just before saccade onset (e.g., Sogo & Osaka, 2002), so we expect that changes in PSD would be most noticeable in our chosen temporal interval. Finally, modeling of sequential flash data (Polá, 2007) suggests that the efference copy signal occurs rapidly and just after saccade onset, so presenting flashes in our range gives the persistent neural response time to develop and overlap with the efference copy signal.

We performed two experiments. In the first experiment we increased the persistence of flashed targets by lowering luminance (Bowen, Pola, & Matin, 1974) to test whether this would affect the PSD for a single-flashed target. We found that PSDs were greater for low than high luminance flashes and that there was a reduction of PSDs for low luminance single-flashed targets presented immediately before the saccade (TSO, 20 ms). In the second experiment we measured PSD with pairs of sequentially flashed targets at different luminances to test the effect of persistence on two-flash interactions described in the literature (Polá, 2007; Sogo & Osaka, 2002). We found a paradoxical pattern of PSDs in which the perceived location of a foveal flash presented further in time from saccade onset actually shifted more than a flash presented closer to saccade onset. In order to account for these results we propose a nonlinear formulation of the persistence-shift model.

General methods

Eye movement recording apparatus

Two dimensional eye position was recorded in Helmholtz coordinates with the video-based binocular Eyelink II tracking system, which has a sampling rate of 500 Hz and spatial resolution limit of 1.5 min arc. The subject’s head was stabilized using a bite bar and forehead rest. Saccade onset time was quantified with a computer algorithm that detects saccade onset with a velocity criterion (>30 deg/s). The stimulus display and eye tracker run on separate (dedicated) computers and we used the timestamps from both to calibrate the eye position data with the stimulus display data. Therefore, the limiting factor in our stimulus setup is the sampling rate (500 Hz) of the eye tracker, making our TSO measurements accurate to within 2 ms. Before each session, gain and linearity of the eye tracker were calibrated for both horizontal and vertical eye positions.

Visual stimuli

Visual stimuli were presented monocularly to the left eye at a 36 cm viewing distance on a 20-inch monochrome monitor (Monoray Model M20ECD5RE; Clinton Electronics, IL, USA), operating at a 120-Hz non-interlaced frame rate with 1024 × 768 pixel resolution. The monitor has a fast DP 104 phosphor, which decays to 0.1% peak in 0.4 ms with a burn-resistant property that is critical to preventing ghost images for flashed stimuli. Rectangular images (1 × 1 deg) were flashed during 1 frame with a 1 ms duration. Subjects were dark adapted before each experimental session for 15 minutes, and a viewpoint in between the subject and the monitor rendered the edges of the monitor invisible so they could not be used as a frame of reference. The background luminance of the display was ≤0.7 cd/m².

Our experiment employed two stimulus conditions. In the single-flashed condition, one rectangle was flashed for 1 ms at 1 degree below the fixation cross prior to a 5 deg leftward saccade at various TSOs. The small 5-degree saccade amplitude was used to enhance estimates of PSDs by placing adjustable post-saccadic probes, used to
estimate perceived location of pre-saccadic foveal-flash test stimuli, within a few degrees of the fovea. In the double-flashed condition, two collinear rectangles, separated vertically by 2 degrees, were flashed sequentially above and below the fixation cross with an inter-stimulus interval (ISI) of 50 ms and duration of 1 ms each. TSO for the double-flashed stimulus is the time between the onset of the second flash and the saccade. The inter-stimulus interval of the double-flashed condition produces unequal PSDs that cause perisaccadic Vernier distortions (PVDs) of the two vertically aligned retinal images (Morrone et al., 1997; Sogo & Osaka, 2002). Test flashes were presented at high and low luminance levels corresponded to 44 cd/m$^2$ and 1.5 cd/m$^2$, where the low-luminance target was near detection threshold. Data for single-flash and double-flash conditions were collected on separate days. The temporal sequence for the double-flash condition was randomized for whether the upper or lower target was flashed first.

**Procedure**

Figure 1A describes the spatial and temporal properties of the double-flash condition. Subjects fixate a small cross at the beginning of a trial. Upon pushing a button, the fixation cross disappeared after a variable delay (580 ms ± 80), and at the same time a saccade target (small cross) was presented 5 degrees to the left of the prior fixation. Subject started to initiate a saccade toward the saccade target. During the latency period of the saccade, two small collinear rectangles were flashed for 1 ms each with an ISI of 50 ms above and below the prior location of the fixation cross. The first flash occurred 90 ms after the onset of the saccade target and the second flash occurred 50 ms after the offset of the first flash. When the second flash disappeared, the fixation cross reappeared and the saccade occurred around this transition. Both the fixation and saccade crosses were visible for several seconds after the second flash disappeared. The computer only accepted trials in which TSOs from the second flash were between 3 and 55 ms. When a trial was accepted, subjects estimated the perceived azimuth of flashed targets by adjusting the horizontal positions of two probes from the test flash screen locations, above and below the fixation point, to screen locations where these flashes had been perceived (Lappe et al., 2000; Sogo & Osaka, 2002). These probes appeared 600 ms after the first disappearance of the fixation cross (400 ms after saccade onset) and the subject’s fixation returned to the original fixation cross while adjusting the probes. The fixation cross and the saccade target served as a sparse frame of reference to estimate the Vernier offsets and PSDs for the sequentially flashed Vernier stimuli. The close temporal proximity of the test flashes and reference crosses facilitated these estimates. Sogo and Osaka (2002) have demonstrated that it is possible to measure perisaccadic Vernier distortions using adjustable probes to estimate the remembered perceived directions of two sequentially

![Figure 1A](image_url)

**Figure 1.** (A) Schematic drawing (left panel) and timing diagram (right panel) of the double-flash condition used in Experiment 2. Subject pressed a button to initiate a trial. The fixation cross disappeared after a variable delay (580 ms ± 80), and at the same time a saccade target (small cross) was presented 5 degrees to the left of the prior fixation. During the latency period of the saccade, two small collinear rectangles were flashed for about 1 ms each with an ISI of 50 ms above and below the prior location of the fixation cross. When the second flash disappeared, the fixation cross reappeared and the saccade occurred within 50 ms after this transition. Both the fixation and saccade crosses were visible after the second flash disappeared. The presence of these crosses then served as a reference for estimating the position of flashed perisaccadic stimuli with adjustable cursor probes (not shown). The single-flash condition in Experiment 1 mirrored the double-flash condition, except that only one of the flashes was presented, located either above or below the fixation cross. (B) Timing of events for the single-flash control condition with delayed fixation reappearance in Experiment 1. In this condition, the reappearance of the fixation crosses was delayed about 500 ms until after the saccade had occurred.
flashed perisaccadic stimuli. Eighty successive trials were performed in a given session and at least 8 sessions were completed for each stimulus.

Analysis

Estimated PSDs were quantified off-line for accepted trials and paired with the TSO on each individual trial. TSO for the first and second flashes differed by 58 ms. PSD is plotted as a function of TSO for the second flash from 3 to 55 ms, which corresponds to a range of TSOs of 61–113 ms for the first flash. All the figures plot apparent position against TSO of the second flash. Scatter plots of raw data are fit with third order polynomials. An example of a function fit to the scatter plot of estimated PSDs against TSO is shown in Figure 2. Functions were compared for various spatio-temporal and luminance conditions.

Subjects

Two of the three subjects were the authors. All three subjects had corrected refractive errors and normal visual acuity, and no history of abnormal binocular vision (i.e., amblyopia, strabismus, uncorrected refractive errors).

Experiment 1: Luminance level and single-flash PSDs

Introduction

The temporal impulse response (TIR) function is a linear model specifying the time course of a neural response to a single flashed stimulus. The persistence-shift model uses TIRs to specify the persistence of the retinal signal. However, studies of ganglion cells at the level of retina and LGN suggest that these cells are nonlinear, and that their TIR function changes with the luminance of a stimulus. Lower luminance energy increases the duration of the TIR (Sperling & Sondhi, 1968; Stromeyer & Martini, 2003) and thus the visual persistence of the object (Bowen et al., 1974). We compared the magnitude of PSDs for single-flashed stimuli with high and low luminances in order to test the hypothesis that the increased duration of the TIR at low luminance levels would increase the magnitude of PSD.

Methods

The single flash condition in Experiment 1 was identical to that used for the double flash condition illustrated in Figure 1, except for the omission of the first rectangle flashed above the fixation point. A single flashed rectangle appeared for 1 ms at 1 degree below the prior location of the fixation target 150 ms after the saccade target appeared. The fixation cross reappeared after the flash ended. The flashed target had either low (near threshold) luminance (1.5 cd/m²) or higher, supra-threshold luminance (44 cd/m²). The data were collected only for flashes that occurred pre-saccadically, and if the observer made any eye movement preceding the flash presentation, that trial was discarded.

Results

PSDs for high and low luminance conditions are plotted in the left column of Figure 3 for the three subjects as a function of TSO. Comparison of PSDs for low luminance (solid lines) and high luminance (dotted lines) conditions illustrates that lowering the luminance greatly increased

![Figure 2. Example of PSD estimates (apparent position) of a single low-luminance pre-saccadic flash plotted as a function of TSO, and a third order polynomial fit to the raw data. All measurements were taken for stimuli that are flashed pre-saccadically (note the negative TSO)—any data in which the observers’ eyes moved before the flash is disregarded.](https://jov.arvojournals.org/content/8/14/22)
the PSD at values of TSO ranging from 5 to 55 ms. The right column will be discussed in the next section. The largest increase of PSD with reduced luminance occurred at TSOs ranging from 10 to 35 ms. This result is consistent with an increased duration of the TIR at low luminance levels, resulting in increased recruitment of the extra-retinal signal.

Discussion

A similar manipulation has been previously reported (Boucher, Groh, & Hughes, 2001), but that study focused on expected latency differences between the neural responses to high and low luminance stimuli. They found a statistically significant effect of luminance, but it was small relative to the predictions of their model. And because their model took into account latency rather than the persistence of the stimuli, it predicted larger differences than the persistence-shift model would expect. Another reason Boucher et al. may not have found a large effect is that the 2 luminance conditions they used were both quite high (4.2 × 10^4 cd m^-2 and 30 cd m^-2). We performed the luminance manipulation with lower luminance stimuli (44 cd m^-2 and 1.5 cd m^-2); so our “high luminance” flash was about as bright as their dim luminance flash. We found a large effect, suggesting that the luminance of the stimuli really does play a significant role in the PSD. Two recent preliminary reports also substantiate the effects of luminance on PSD (Georg, Hamker, & Lappe, 2007; Zhang, Cantor, & Schor, 2007).

A second and surprising result of this experiment was that the PSD for the low luminance flash declined markedly at very short TSOs to values similar to PSD at the high luminance level. Our result is not necessary a contradiction of previous studies, even though the literature has traditionally assumed that peak mislocalization occurs at saccade onset. A number of studies report data...
that can be interpreted as showing a decrease in PSD for objects flashed closer to saccade onset. For example, close inspection of Sogo and Osaka’s double flash data reveals that the PSD for 0 TSO was lower than for their smallest TSO of 10 ms, while Honda’s (1991) time courses for perisaccadic mislocalization also appear to peak prior to saccade onset, and Awatere and Lappe (2004) computed a perisaccadic shift index that peaked well before saccade onset in conditions of darkness.

However, despite the existence of these data in the literature, the possibility and cause of a pre-saccadic decline in PSD has not been previously considered. We believe that a decline in PSD at short TSOs could be due to saccadic suppression, which has been shown to shorten the TIR (Burr & Morrone, 1996). Saccadic suppression begins 50 ms before the saccade and persists 50 ms after completion of the saccade (Zuber & Stark, 1966). During this period, detection thresholds are elevated 0.5–0.7 log units, and saccadic suppression has a greater effect on reducing visibility of low than high luminance stimuli (Zuber & Stark, 1966), which could explain why the decline is so apparent for low luminance stimuli.

An alternate explanation could be that the decline of PSD at short TSOs results from temporal interactions with the reappearance of the fixation cross when the flash was extinguished. Indeed, reference cues that appear before the saccade have been shown to influence the magnitude of PSD (Lappe et al., 2000). To test the influence of these reference cues, we performed an additional control experiment on two subjects for the low luminance flash. Subjects confirmed that their subjective experience was that flashes were always visible.

The outcomes of these control experiments suggest that the reduction of PSD near saccade onset is not an artifact of backward masking or reduced visibility. It is replicated in the sequential “double-flash” results in Experiment 2 and has profound implications for the modeling of PSD. We will discuss saccadic suppression and its modeling after we report the results of this second experiment.

### Experiment 2: Interactions for pairs of flashed stimuli

#### Introduction

When two flashes are presented sequentially around the time of a saccade, their PSDs cannot be predicted on the basis of single-flash PSD (Sogo & Osaka, 2002). This suggests that the two flashes interact with one another, such that perceived position is altered by temporally or spatially proximal stimulation. A recent version of the persistence-shift model (Polha, 2007) explained this interaction through a mechanism operating on the temporal overlap of the TIRs of both of the flashed stimuli. When the persisting neural responses of the two flashes overlap, the model pulls their perceived positions toward one another. Consequently, the model produces a larger PSD for the earlier flash and a smaller PSD for the later flash than if they had been presented singly. We made sure that we could reproduce this effect in our stimuli and investigated the effects of flash persistence and overlap on the interaction between sequentially flashed perisaccadic stimuli, varying the overlap of the TIRs by changing the relative luminance of the two flashes.

Whereas Sogo and Osaka (2002) manipulated the interactions by changing the ISI of two flashes, we maintained a shorter ISI at 50 ms and changed the luminance values of the flash pair instead. By choosing a shorter ISI than Sogo et al. (50 vs. 80 ms), we expected to increase overlap between flash persistence and thus maximize interactions. We used the luminance values from Experiment 1 and tested with sequential double-flash stimuli for 4 luminance value combinations (low–low, high–high, high–low, and low–high). This manipulation was construed as a test of the persistence-shift model, because changing the luminance level while keeping the ISI constant should be expected to change the overlap of the impulse responses of the flashes. Temporal overlap, and therefore interaction, should be greatest when the first flash has low as opposed to high luminance.

**Experiment 2** also asks whether changes in flash persistence (possibly due to saccadic suppression and luminance) have more of an effect on PSD than the temporal interactions between the two flash stimuli, as described by Polha (2007). We expect the luminance and temporal (TSO) effects seen in **Experiment 1** to occur for
two-flash stimuli, with each flash undergoing smaller PSD at high as compared to low luminances. However, interaction between two flashes might have more of an effect than luminance of the stimuli, or could even change the luminance dependence itself, and this experiment allows us to examine that possibility.

**Methods**

The procedures for the double-flashed conditions were the same as described in the General methods section and the spatial and temporal properties of the stimuli are illustrated in Figure 1A (left and middle panels). Data were collected for TSOs for the second flash ranging from 3 to 55 ms. The 50 ms ISI is shorter than the shortest ISI used in prior studies of periscadic Vernier distortions (75–80 ms; Morrone et al., 1997; Sogo & Osaka, 2002), in order to exaggerate any spatio-temporal interactions between successively flashed stimuli. As in Experiment 1 a high luminance flash measured 44 cd/m² and a low luminance flash measured 1.5 cd/m².

**Results**

Figure 4 plots the results of Experiment 2 for three subjects in the four luminance conditions. The results have been plotted to facilitate comparison of the PSD magnitudes of the first and second flashes. The x-axis values specify the TSO for the second flash and we have aligned the data so that we can observe the differences in PSD experienced for the first flash (solid blue line) as opposed to the second flash (dotted red line). Readers should keep in mind that each first flash data point has shifted by 58 ms in order to line up these plots.

**High–high and low–low luminance conditions**

Comparison of the high–high with the low–low condition (top half of Figure 4) reveals that overall PSDs were higher for both flashes at all TSOs for the low–low condition. These results are consistent with general trend in single-flash results shown in Figure 3, where lowering luminance increased PSD. Comparing PSDs of these equal-luminance flash pairs also offers a way to looking at the drop-off in PSD seen for low luminance flashes as TSO decreased (Figure 3), since the flashes are spaced 50 ms apart. With both our low and high luminance stimuli, Figure 4 illustrates a reduction of PSDs for the second flash at short TSOs.

**Crossover paradox**

The reduction of PSD at small TSOs (>10 ms) is so great that pairs of plots in Figure 4 actually crossover one another. Because there is no reduction of PSD for the first flash at either luminance level at its shortest TSO (58 ms), we conclude that the reduction of PSD for the second flash depends on a combination of both low luminance and a short TSO. We also note that crossover is more pronounced in the low–low as opposed to the high–high condition. As PSDs of single flashes have been previously reported to increase with temporal proximity to the onset of the saccade (Honda, 1991) it is paradoxical to find a condition in which the perceived shift is greater for the first flash than for the second flash. Although we think that a general decline in PSD at low TSO, as well as crossover for paired flashes, has been hinted at by data in other studies, one reason it may have remained unnoticed is because ISIs employed in previous double-flash studies were much larger than our 50 ms (e.g., Sogo and Osaka’s shortest ISI was 80 ms) and because PSD studies did not focus on the short pre-saccadic temporal intervals we have examined here.

**High–low and low–high mixed luminance conditions**

The left and right lower panels of Figure 4 compare the high–low and low–high mixed luminance conditions. When the luminance of the second flash was lower than that of the first (left lower panel) PSD was larger for the second flash at all values of TSO. When the first flash luminance was lower than that of the second flash (right lower panel), there was an exaggerated reversal of PSD amplitudes over a larger range of TSOs than was found with the equal luminance stimuli shown in the upper panel.

**Interactions between paired flashes**

Our results confirm Sogo and Osaka’s observation that the early flash is shifted more in the saccade direction and
the later flash is displaced less in the same direction as the saccade than if either flash had been presented alone (Sogo & Osaka, 2002). Panels A and B in Figure 5 plot the PSD (in high and low luminance conditions) for a single flash alongside the PSD for the same flash when a second paired flash is presented. This comparison shows that our double-flash data could not be predicted by the data we had taken in the single-flash experiment. For both high and low luminance stimulus conditions, the second of two paired flashes moves significantly less than it would if it were presented alone, while the PSD of the first flash is enhanced due to the subsequent presentation of a paired flash. Data from all 4 conditions (equiluminant and mixed luminance) in Experiment 2 is combined in panels C and D, and the interaction is quantified as change in PSD measured for a given flash when we increase the persistence of its companion flash (decrease the luminance). Panel C plots PSD with a low luminance companion flash condition minus PSD with a high luminance companion flash. The black open circles, for example, show the first flash PSD in the L–L condition minus the first flash PSD in the L–H condition. Panel D normalizes the absolute differences in (C) by dividing each plot by the sum of PSD for the two conditions. This percentage plot shows how big the change in PSD is relative to the shift magnitudes occurring at a given TSO. Positive values suggest increasing persistence of the companion flash enhances PSD and negative values suggest increasing persistence of the companion flash lowers PSD. Zero values (dotted line) indicate no interaction, so there is interaction at almost every TSO. The first flash PSD is usually enhanced by increased persistence of the second flash, while the second flash PSD decreases when the preceding flash has a long persistence. We speculate that the crossover of these plots for high luminance flashes is related to the effects of saccadic suppression (see Figure 6).

Panels C and D in Figure 5 provide a different look at paired flash interactions to specifically examine the effects of luminance-dependent persistence changes. Plots are of the difference in PSD between the low and high luminance conditions for either the first or second flash. Each curve plots a 3 subject average (for a given flash) of change in PSD for either the first or second flash when the persistence of its companion flash is increased by lowering its luminance. For example, positive values for the “first-low” condition indicate that a low luminance first flash shifted more when it was paired with a low luminance second flash (as opposed to a high luminance second flash). The plots in Figure 5C represent the
Discussion

Results from Experiment 2 confirmed the outcome of the single flash experiment. Lowering the luminance of targets (increasing persistence) produces a larger PSD. Comparing Figures 3 and 4, the curves in Experiment 2 are quite similar to the curves in Experiment 1. In the low—low condition, PSDs were generally higher than the high—high condition. This is consistent with increased persistence causing greater recruitment of the extra-retinal eye position signal during position estimation in the low luminance conditions. Mixed conditions also produced an expected result based on the single flash experiment.

Our results also confirm the presence of interactions in the two flash condition. The pattern of these interactions is consistent with the persistence-shift model described by Pola (2007), in two respects. First, it reinforces the idea that the increased persistence of targets allows for greater interactions between the two flashes. Figure 5B confirms that first flashes shift more and second flashes shift less when the companion flash has a lower luminance/longer persistence as opposed to a higher luminance/shorter persistence. In other words, paired flash interactions are enhanced by increasing persistence. Second, we note that just as single flashes are shifted less at higher luminance and just before saccade onset, there is a concomitant reduction in the interaction between the two flashes. Specifically, interactions between flashes are greater for low luminance flashes and are reduced or even reversed at low TSOs. This is consistent with the Pola’s formulation of interaction as a second stage acting as a sort of gravity between perceived position of flashes. When TSO or luminance causes the single flash position shift to be less dramatic, this also reduces its influence on the companion flash.

As the interactions between two flashes are consistent with the persistence-shift model described by Pola, we do not consider them to have a significant influence on the crossover phenomenon demonstrated with two flash stimuli. In Pola’s model, perceived positions of paired flashes gravitate toward one another, and this gravitation does not account for a reversal (crossover) in perceived relative position. This crossover and how it relates to saccadic suppression will be discussed in the General discussion section.

General discussion

The persistence-shift model of PSD relies on the temporal duration of the visual response to the stimulus (Pola, 2007). When this persistence overlaps with the extra-retinal eye-position signal, the perceived visual direction of a foveal stimulus shifts in the direction of the subsequent eye movement. Our results are consistent with the hypothesis that stimulus characteristics known to modify the temporal impulse response will also modify the amplitude of PSDs, and thus confirm the general predictions of the persistence-shift model.

The first stimulus factor to consider is the effect of luminance on the TIR. The literature contains numerous reports—both psychophysical (e.g., Bowen et al., 1974; Stromeyer & Martini, 2003) and physiological (e.g., Kaplan & Benardete, 2001)—that indicate that persistence depends on stimulus energy. Brighter stimuli undergo a shorter temporal integration because they produce a larger magnitude response from early visual mechanisms. By contrast, the response to dimmer stimuli persists for a longer period in order to compensate for their smaller response. Our first experiment showed that PSDs for single flashes were indeed larger for low-luminance stimuli, as we would expect from a longer duration response in the persistence-shift model.

Interestingly, previous reports (Boucher et al., 2001) concluded that luminance was a negligible factor in producing PSDs. While Boucher et al. did find a statistically significant but small effect of luminance on PSDs, the importance of this result was downplayed because the measured effect did not match the predictions of their model. However, it has been argued that their model may overestimate the effects of luminance because it predicts PSD on the basis of the latency of neural response and not its time course (Pola, 2004).

Furthermore, it appears that stimulus differences between our study and Boucher’s study (see Introduction section of Experiment 1) are responsible for the different effects of luminance on PSD amplitude found in the two studies. Our stimuli probed a different (near threshold) luminance level and we did find a powerful effect of luminance on the amplitude of the PSD. This suggests that our stimuli may have produced a larger increase in duration of the TIR than their stimuli (their low luminance flash was approximately equal to our high-luminance flash). Other studies (Georg et al., 2007) have also reported increased PSDs resulting from near-threshold stimuli, and our view is that these luminance effects are a strong prediction of the persistence-shift model.

Finally, we note that there are discrepancies in PSD magnitudes for seemingly minor stimulus differences. For example, Honda (1991) asked observers to localize flashed objects at close to our (high) luminance values, at the same location in the visual field, but recorded (proportionally) larger PSDs for 8 degree vertical saccades.
The magnitude of pre-saccadic PSDs for our high luminance condition peak around 20% of the saccade amplitude while his study shows peak magnitudes of around 35%. But this discrepancy could be due to a number of stimulus factors. First, Honda’s flashed objects were less than half the size of ours, so we might consider them to be less effective in shortening the persistence of the TIR. The fixation spots that Honda used to control eye movements were dimmer than the fixation spots used in our study, and Honda used different colors for the fixation spots (red) and flashed objects (yellow) LEDs. These differences might have indirectly affected the PSD magnitude, as perceived location of visual references present on the screen can themselves shift and their perceived locations may cause interactions similar to those seen with sequentially flashed pairs of stimuli. Examples of such effects are mislocalizations of the fixation spot used as the saccade target (Awater & Lappe, 2006) and changes in PSD induced by the adaptation state of the observer (Georg, Hamker, & Lappe, 2008). Thus both stimulus differences and the effects of different visual context or background could produce discrepancies between PSDs reported in different studies.

Next, we consider the effects of saccadic suppression on the TIRs produced by the various stimulus conditions. To our knowledge, our study is the first to incorporate saccadic suppression in a model of PSD. Saccadic suppression could influence PSD by reducing visual sensitivity for a period of time beginning approximately 50 ms before saccade and ending after saccade completion (Diamond, Ross, & Morrone, 2000; Zuber & Stark, 1966). It occurs at early stages in visual processing (Sylvester, Haynes, & Rees, 2005; Thilo, Santoro, Walsh, & Blakemore, 2004; Usrey, Reppas, & Reid, 1999) and results in compression and gain reduction of the TIR (Burr & Morrone, 1996). Since compression of the TIR reduces the duration of flash persistence, it should reduce the magnitude of PSD for stimuli flashed just before the saccade onset. We found evidence supporting the predicted roll-off of PSDs at short TSOs with low luminance stimuli but did not find it for high luminance stimuli. We might expect, however, to find more saccadic suppression with low than high luminance targets as was demonstrated by Zuber and Stark (1966). Because the TIR for a low luminance stimulus persists longer, it should show more of an effect of suppression. And, because PSD magnitude is enhanced for low luminance stimuli, a roll-off in the amplitude of the effect would be more visible with low than high luminance stimuli.

We performed an additional control experiment to verify whether saccadic suppression was occurring in our experiments. Because controls run for Experiment 1 verified only that our stimuli were always visible, we had to use less visible stimuli to test for the presence of saccadic suppression. While fixated, subjects performed a pure detection task (present/not present) using a QUEST staircase to determine absolute luminance and decrement contrast thresholds for 75% detection of our flashed stimuli (spatial and temporal configurations of our stimuli were the same as used in Experiment 1). For a pure luminance increment we derived a threshold of 0.4 cd/m² on a dark background, and for a light decrement on a 1 cd/m² background we derived a Weber fraction detection threshold of 10–15%. Stimuli at these threshold values were used while subjects made 5 degree saccades and repeated the luminance and contrast decrement detection tasks. We measured detection performance for two subjects. In the absolute luminance detection task, we found no significant effect of TSO on detection performance, but when the luminance decrement stimulus was used, we found that performance dropped for TSOs lower than 30 ms. We interpret these results as evidence that saccadic suppression was present in our subjects at the TSOs we tested, and that it could have reduced the duration of the impulse response function for the significantly above-threshold flashes that we used to measure PSDs.

This result is interesting in light of previous work that suggests that saccadic suppression has an effect on the perceived spatial compression but not the uniform shift experienced during saccades (Michels & Lappe, 2004). That study used contrast defined stimuli and reported that suppression both reduced visibility for low-contrast stimuli and was responsible for a change in the magnitude of compression. However, stimulus contrast did not affect the shift component of PSD. By contrast, visibility of our luminance stimuli remained constant, and we found a reduction of the shift in PSD for short TSOs that we attribute to changes in visual persistence caused by saccadic suppression. The importance of luminance or “stimulus strength” in producing a “shifted” PSD (see also Georg et al., 2007; Zhang et al., 2007) may indicate that there is a substantial difference between the processes that generate perisaccadic spatial compression and those that generate perisaccadic shift. Perhaps compression is a process that operates on contrast of a stimulus (visibility) whereas the perisaccadic shifts are due to a process that combines stimulus persistence (TIR) and the extra-retinal eye position signal (e.g., the persistence-shift model).

Saccadic suppression is a parsimonious explanation of an otherwise paradoxical observation about the dependence of PSD on TSO. Unlike previous studies which suggest PSDs of single flashes increase with temporal proximity to the onset of the saccade (Honda, 1991), we found that with paired flashes presented in the same trial, the second flash appeared to move less than the first flash when they occurred close to saccade onset. For example, in the low–low condition, the perceived position of a flash occurring 63 ms before the saccade usually overtook the perceived position of a flash presented 5 ms before saccade offset. To visualize this crossover effect in Figure 6, we plot the percentage of all double-flash trials in which observers reported that the first flash moved more than the second. Each of the 4 plots shows this percentage as a function of TSO for one of the four double-flash
luminance conditions. When the value is above 50% (dotted horizontal line), the perceived position of the first flash has overtaken that of the second. If there was no reversal of perceived position, points should always remain below the dotted line. At the largest TSOs, this is the case, and the first flash is always seen shifted less than the second. However, as TSO decreases, in three conditions there is nearly a 100% reversal of the perceived relative position of the two flashes.

Figure 6 confirms the expectations of the persistence-shift model when the effects of the different luminance conditions are considered in relation to one another. In the low–high condition (circle symbols) the first flash (with greater persistence) overtakes the second much sooner (at longer TSOs), and by a great amount at low TSOs. By contrast, in the high–low condition (triangle symbols), the first flash has much shorter persistence and thus fails to recruit more of the eye position signal. The difference between the PSD for first and second flashes in this condition is bigger than in any other condition, and as a result the first flash never overtakes the second flash. While our results are consistent with the interactions described in the persistence-shift model (Pola, 2007) it is important to note that the interaction mechanism described in his paper cannot account for a crossover in the perceived position of two flashes that is shown in Figure 6. That model proposes an interaction between the perceived position of each of the flashes is based on the temporal overlap of their respective TIRs. When the beginning of the second flash response overlapped the end of the first flash response, the first part of the position estimate of the second flash biased the perceived position estimate of the first flash and enhanced it relative to a corresponding single-flash PSD. Likewise, the end of the retinal signal of the first flash overlapped the beginning second flash response. That last portion of the position estimate for the first flash shifted the estimate of the position signal for the second flash away from the saccade and reduced its PSD. However, our data (Figure 6) demonstrates a reversal of the direction of vernier offset between two (aligned) perisaccadic-foveal targets. Because the interaction described by the persistence-shift model amounts to pulling the position signals of each flash toward one another, the maximum effect of such a positional gravitation would be to superimpose the position estimates of the two targets, and the pulling would not reverse the order of their spatial positions. Instead, saccadic suppression is likely to be primarily responsible for the reversal, since it disproportionately affects the second flash. Therefore, we believe that the crossover is based mostly on TSO and luminance, which influence the position of single flashes the same way as they influence the position of double flashes.

A final stimulus factor that we considered is an interaction between paired flashes. We believe that the model of interactions given by Pola (2007) can account for the interactions we saw. However, the reduction of PSD for the second of two paired flashes might also be explained by contrast gain control (CGC). Studies of visual persistence (Kanai & Watanabe, 2006) and masking (Snowden, 2001; Solomon, Lee, & Sun, 2006) demonstrate that the visual response to a stimulus can be modified by a second stimulus that is presented in close (temporal or spatial) proximity. In particular, a preceding stimulus can shorten the temporal impulse response of a successive stimulus (Stromeyer, 2003). This CGC is a localized and fast process that modifies the response dynamics of neurons (Wilson & Kim, 1998).

Moreover, saccadic suppression need not occur independent of contrast gain control. It has been suggested that
A. Model schematic

- First flash
  - Temporal impulse response
  - Rectification
- Second flash
  - Temporal impulse response
  - Rectification
- Saccadic suppression

B. Temporal impulse response profiles

- First high, second low
- First low, second high
- Gain control
- Saccadic suppression

C. Single TIR predictions

- PSD vs. TSO
  - Low vs. High

D. Single flash luminance

- PSD vs. TSO
  - Low vs. High

E. Double vs. single flash

- PSD vs. TSO
  - Single flash vs. Double flash

F. Saccadic suppression

- PSD vs. TSO
  - Suppression signal
  - First flash vs. Second flash
the mechanism for saccadic suppression occurs through a common mechanism in the LGN (Ross, Burr, & Morrone, 1996; Usrey et al., 1999). Further support for such a mechanism can be found in electrophysiological studies where simulated saccades in the suppressive field of LGN neurons produced an effect comparable to contrast gain control (e.g., Felisberti & Derrington, 2001). In this view, CGC and saccadic suppression can both be described by a single nonlinear modulation of the TIR—a gain reduction coupled with an increasingly biphasic and compressed TIR. These observations have prompted us to examine the effects that such nonlinear modifications would have on the persistence-shift model. The next section examines the consequences saccadic suppression and contrast gain control could have on the position signal interaction in the persistence-shift model.

**Nonlinear modifications to the persistence-shift model**

Of the effects described in this discussion, previous versions of the persistence-shift model (Pola, 2004, 2007) can account for increased PSD at low luminance and even for the crossover effect when we used unequal luminance stimuli (e.g., our low–high condition). However, unless it incorporates TSO dependent mechanisms, the model cannot predict a drop-off in PSD just before saccade onset, nor the related crossover effect in equal luminance conditions. This section examines what would happen if we implemented TSO-dependent nonlinearity in the model to simulate the effects of saccadic suppression.

Our formulation changes the TIR for a given flashed stimulus based on its TSO, and also based on its luminance and the masking effects of a previous flash (CGC). Our intent is not to fit data or do quantitative comparisons with previous versions of the model, but rather to demonstrate the patterns of stimulus dependence that a nonlinear formulation can predict. All simulations were implemented using MATLAB.

We refer to our formulation as the nonlinear persistence-shift model for the purposes of this discussion. The nonlinear components are:

1. The TIR for individual flashes varies with luminance.
2. Contrast gain control compresses the TIR of the second flash, reduces its gain, and makes it more biphasic.
3. Saccadic suppression changes the TIR of the visual system within 50 ms of the saccade.

These proposed modifications of the persistence-shift model are based on mechanisms that have been described as early as retina/LGN and have been shown to affect the TIR for visual stimuli. We refer to this version of the model as the nonlinear persistence-shift model (Figure 7A).

The model takes two brief pulse signals \( I_1(t) \) and \( I_2(t) \) as input and convolves them with separate TIR functions \( f_1(t) \) and \( f_2(t) \).

\[
R(t) = \int I(t)f(t-t')dt. \tag{1}
\]

Each temporal impulse response function is derived by differentiating a “generator” function \( h(t) \) following Fredericksen and Hess (1998). The formulation depends on three parameters, \( a, \beta, \) and \( \gamma \):

\[
h(t) = e^{-\left(\frac{t}{\tau_a}\right)^2}, \quad f(t) = \gamma \left[ \frac{\partial (h(t))}{\partial t} \right]. \tag{2}
\]

\( a \) specifies the duration of the function, \( \beta \) is the biphasic index, specifying the magnitude of the inhibitory component, and \( \gamma \) is the amplitude of the TIR. \( \gamma \) remained unchanged at 1 in these simulations. \( R_1(t) \) and \( R_2(t) \) correspond to the retinal signal and the persistence of each of the flashes. These retinal signals are used to compute a weighted average of the extra-
retinal eye position signal $e x R(t)$, producing a position estimate:

$$P = k \int_{t_a}^{t_b} R(t) e x R(t) \, dt,$$

(3)

where $t_a$ and $t_b$ specify the onset and offset times of the “retinal” response to the flash. We model the extra-retinal signal as a cumulative sum of a Gaussian.

$$e x R(t) = \int_{-\infty}^{t} \frac{1}{\sqrt{2\pi} \sigma} e^{-\frac{(t-\mu)^2}{2\sigma^2}}. \quad (4)$$

The latency of this signal can be specified by the time (relative to saccade onset) at which it reaches 5% of its final value. In our simulations, this occurs at 23 ms. The signal reaches 95% of its final value by 56 ms after saccade onset. It is therefore a relatively fast signal (close to actual saccade dynamics) that is slightly delayed relative to saccade onset.

To this point, the model we have described is functionally equivalent to the persistence-shift model as previously described in the literature (Pola, 2007). The nonlinear modification we propose allows the TIR functions to differ from one another and also to change from one moment to the next. There are three ways to reduce the values of $\alpha$, $\beta$, and $\gamma$:

1. increased stimulus luminance,
2. having the second target influenced by contrast of the first of a pair of targets (CGC), and
3. saccadic suppression at small TSOs.

Changes to the TIR parameters alter the time course of the functions $f_1(t)$ and $f_2(t)$ and thus the persistence of the neural response and the resultant PSD.

These modifications occur in two stages. First, we make the assumption that the effects of luminance and contrast gain control on the TIR are independent of the TSO at which the flashes are presented. In other words, the luminance of the flash and its order of presentation determine a base TIR of the system, fixing a set of parameters that will specify the same TIR at every TSO. This process is depicted in the model schematic in Figure 7A, in the output of the luminance and CGC boxes. Second, in order to model saccadic suppression we generate time dependent changes in the TIR that are determined by the TSO. We introduce a rapid suppressive signal $S(t)$ that operates as a suppression of the TIR parameters produced by the input stimulus qualities. When $S(t)$ is 1 there is a maximal suppression of the TIR. In this formulation we used a raised cosine window (“tukey window” in MATLAB, $\alpha = 0.5$) that could be fully specified by its temporal interval (starting and ending times).

The time course we have chosen for our suppression was approximated in an effort to match the time course of suppression that has been reported in the literature. We used the same window size for all Figures 7D–7F, spanning a TSO range of $-47$ to $+150$ ms. In our model, these values produce a suppressive signal that starts about 50 ms before saccade onset and is maximal at the time of saccade onset (e.g., Diamond et al., 2000; Michels & Lappe, 2004). An example of the time course of saccadic suppression in our model and its effects on PSD can be seen in Figure 7F. Saccadic suppression follows the black dashed line and is plotted alongside the magnitude of the PSD for the first and second of two paired flashes.

Figure 7A shows a schematic illustration of the non-linear persistence-shift model. In order to reduce clutter, we only depict nonlinear mechanisms operating on the bottom input ($I_2$), but the nonlinear model implements the same modifications for both inputs. Figure 7B illustrates the modifications accomplished in the model, by plotting different retinal signals that could result from stimulus pulse pairs. The first two panels in Figure 7B show that the persistence of the first flash overtakes that of the second when it has a low enough luminance and that the luminance effect occurs regardless of the order of the flashes. The third panel shows a (relatively) small suppressive effect that the first flash has on the TIR of a second flash luminance. This is the function of contrast gain control in the model. The fourth panel shows the effect of saccadic suppression on the TIR. We have added the extra-retinal signal (black sigmoidal curve) for reference, since this effect only occurs near the time of the onset of a saccade. We consider the effect of saccadic suppression to be much stronger than the effect of contrast gain control and we believe that it produces the paradoxical effect discussed earlier, when the first flash overates the second (see also Figure 7F).

Figure 7C illustrates the behavior of a persistence-shift model for TIRs that remain constant with TSO. In the TIR module boxes in Figure 7A we depict a family of TIR functions that can be generated by manipulating the parameters $\alpha$, $\beta$, and $\gamma$. The curves in Figure 7C are snapshots of the model output with each of these TIR functions. Note that while different PSDs are generated by each of the TIRs at each TSO, the results illustrate that no matter which TIR function is used, a model that does not allow the TIR to change always produces a PSD magnitude that increases as the TSO gets smaller. However, since our data shows a decline in PSD as TSO gets close to zero, we conclude that some TSO-dependent modification of the model is necessary to produce PSDs that decrease near saccade onset.

The orange dot trajectory through Figure 7C illustrates how PSD could change if the TIR was modified by nonlinear interactions. In the nonlinear model, points can come from any of these curves, so that at large TSOs where there is no saccadic suppression, the points come from a curve corresponding to a long-persistence TIR. As
the TSO decreases, the TIR switches to a shorter persistence and the corresponding curve determines the PSD. So while an individual TIR function will only produce a PSD that increases with shorter TSOs, a nonlinear modification involving a family of TIR functions can generate a PSD that declines at short TSOs.

Panels D–F plot predictions of the nonlinear persistence-shift model. These are not, however, fits to our data. The model is highly sensitive to all of the parameters and we prefer to examine the pattern of results when most of these parameters are fixed and only a few are varied. Each of these three panels shows the predictions of the nonlinear model for the perceived position of the flashes (PSD) as a function of TSO. Note that for a given TSO, if the retinal signals do not overlap the extra-retinal signal, the model predicts no distortion (PSD = 0). Also, in order to focus on the effects of changing the TIR, Figure 7 does not take interaction between flashes into account and omits the effects of interaction proposed by Pola (2007).

The different data plots in panels D–F are generated by changing only the TIR parameters for each of the flashes. Other model parameters remain constant. Since the TIRs are allowed to change over time, each parameter is defined as a range, which is then sampled at a given TSO based on the value of the saccadic suppression signal. In panels D and E, the parameter ranges for the two TIRs are different, to indicate the effects of shortening one TIR relative to another. In panel F, the TIR ranges are the same for both of the flashes, and the plots are shifted to show how saccadic suppression will cause the earlier flash to overtake the later one.

Figure 7D shows the effects of luminance on PSD for single flashes differing in luminance. The green line shows the PSD for a high luminance flash and the red line shows the results for a low luminance flash. Because the high luminance flash produces a shorter TIR than the low luminance TIR, the resultant PSD is lower in the high-luminance condition. The parameters for the low luminance flash are chosen such that when suppression signal was 0, \( \alpha = 200 \text{ ms} \) and \( \beta = 1.6 \). The low luminance TIR parameters are reduced to \( \alpha = 45 \text{ ms} \) and \( \beta = 0.4 \) when the saccadic suppression signal was 1. Meanwhile, the parameters for the high luminance flash are chosen such that the unsuppressed high luminance TIR is significantly shorter than the unsuppressed low luminance TIR: \( \alpha = 120 \text{ ms} \) and \( \beta = 1.4 \), when saccadic suppression is 0. These parameters are reduced at full saccadic suppression to \( \alpha = 45 \text{ ms} \) and \( \beta = 0.4 \). Notice that there is a resultant sharp drop-off in the PSDs at low TSOs, especially for the low luminance flash. This is the effect of the saccadic suppression, which is more significant for the low luminance flash because its TIR starts out as longer. Figure 7E illustrates how this saccadic suppression produced crossover for double-flash stimuli.

Figure 7F illustrates the effects of contrast gain control (CGC) by juxtaposing the predicted PSD for a single high-luminance flash with the PSD for the second of a pair of flashes. Whereas the TIR for both stimuli would be the same in the linear model, in this nonlinear model, the response of the first flash reduces the persistence of the second flash through the process of contrast gain control. As with luminance, this CGC-mediated reduction of the TIR is independent of TSO. We have assumed that the effects of CGC are much smaller than the effect of luminance based on our data. This panel shows that when the TIR is changed slightly to account for this interaction, the PSD for the second paired flash (green line) shows only a slight reduction in magnitude. The first flash TIR parameters were kept the same as the high luminance flash in the previous paragraph: \( \alpha = 120 \text{ ms} (45 \text{ ms}) \) and \( \beta = 1.4 (0.4) \) when the suppression signal was 0 (1). The second flash parameters were very slightly reduced by CGC, with \( \alpha = 110 \text{ ms} (45 \text{ ms}) \) and \( \beta = 1.3 (0.4) \) when the saccadic suppression signal was 0 (1).

Figure 7F shows the surprising effects of saccadic suppression. The previous examples considered flashes at equal TSOs, whereas this plot shows the PSD for the first and second of two paired flashes. It is important to keep in mind that the \( x \)-axis of the first (early) flash has been shifted in order to superimpose the paired sequential flashes. In other words, the TSO for the first flash in this plot (red line) is actually 50 ms greater than that of the second flash. The paradox is that the PSD of a stimulus at 5 ms is overtaken by the PSD of a stimulus preceding it at 55 ms. We reiterate that two-flash interactions and luminance dependence in the persistence-shift model cannot account for this crossover effect. But by allowing the TIR to undergo a simulated saccadic suppression, a nonlinear persistence-shift model will generate a crossover effect. The TIR values for both flashes in this example were chosen such that \( \alpha = 200 \text{ ms} \) and \( \beta = 1.6 \) when the saccadic suppression signal was 0 and \( \alpha = 45 \text{ ms} \) and \( \beta = 0.4 \) when the saccadic suppression signal was 1.

Our simulations did not manipulate the duration or latency of the extra-retinal signal, which are highly interdependent with TIR to produce a given PSD. For example, a larger latency of the extra-retinal signal requires a longer retinal signal persistence for the same TSO to generate a shift in perceived position. We have generated these figures to show that the robust paradoxical interactions that occur for perisaccadic flash pairs at short TSOs can be accounted for by nonlinearities in low-level visual mechanisms.

It is also important to note that the nonlinearities in our model formulation do not predict enhancements of the first flash PSD (see Figure 4). However, the interactive component of the persistence-shift model can predict that enhancement. We also note that enhancement of the first flash is relatively small when compared to the effects of lowering luminance, or when compared to the crossover produced by saccadic suppression in the nonlinear model. Nevertheless, the nonlinear formulation is not in conflict with the persistence-shift model, and together they provide a parsimonious account of the spatial distortions of perisaccadic foveal stimuli.
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