Masking the saccadic smear

Marianne Duyck Laboratoire Psychologie de la Perception, Université Paris Descartes and Centre National de Recherche Scientifique, Paris, France

Thérèse Collins Laboratoire Psychologie de la Perception, Université Paris Descartes and Centre National de Recherche Scientifique, Paris, France

Mark Wexler Laboratoire Psychologie de la Perception, Université Paris Descartes and Centre National de Recherche Scientifique, Paris, France

Static visual stimuli are smeared across the retina during saccades, but in normal conditions this smear is not perceived. Instead, we perceive the visual scene as static and sharp. However, retinal smear is perceived if stimuli are shown only intrasaccadically, but not if the stimulus is additionally shown before a saccade begins, or after the saccade ends (Campbell & Wurtz, 1978). This inhibition has been compared to forward and backward metacontrast masking, but with spatial relations between stimulus and mask that are different from ordinary metacontrast during fixation. Previous studies of smear masking have used subjective measures of smear perception. Here we develop a new, objective technique for measuring smear masking, based on the spatial localization of a gap in the smear created by very quickly blanking the stimulus at various points during the saccade. We apply this technique to show that smear masking survives dichoptic presentation (suggesting that it is therefore cortical in origin), as well as separations of as much as 6° between smear and mask.

Introduction

Any model of vision which takes the retinal image as a starting point immediately runs into the problem of eye movements, and in particular saccades. Although saccades lead to frequent, rapid displacements of the retinal image, the retinal consequences of these displacements are largely not perceived. The saccade-induced effects on the retinal input may be classified into two categories, intra- and trans-saccadic. Intrasaccadically, the optic array translates rapidly across the retina. Even at maximal saccadic speeds (300°–800°/s for saccades of 10° or more), very low spatial frequencies in the image should be perceived clearly and in motion (Burr & Ross, 1982). Gratings perpendicular to the saccade with higher spatial frequencies, on the other hand, should be perceived as smeared at these speeds (Barlow, 1958). Trans-saccadically, the same object impinges on different retinal locations before and after the saccade. Under the usual conditions, none of these retinal modifications is perceived: The world is perceived as sharp, immobile and stable, which raises two questions. First, how does the visual system achieve stability based on discontinuous input (Wurtz, 2008) and second, why don't we perceive the retinal smear, also known as blur or gray-out, that results from saccades? In this paper we address the second question, sometimes known as saccadic omission.

Saccadic omission has been linked to the phenomenon of saccadic suppression, a drop in visual sensitivity starting roughly 50 ms before a saccade and lasting until the end of the saccade. Two general hypotheses have been proposed to account for both saccadic omission and suppression (see Wurtz, 2008; Castet, 2010; Higgins & Rayner, 2014, for recent reviews): an active mechanism of central origin that would inhibit visual processing early on; and a passive, purely visual origin.

The central mechanism theory is appealing, especially with the idea that the magnocellular pathway, particularly involved in motion processing, may be specifically and centrally suppressed during saccades (Burr, Morrone, & Ross, 1994). More recent studies suggest, however, that motion can be perceived during

Citation: Duyck, M., Collins, T., & Wexler, M. (2016). Masking the saccadic smear. *Journal of Vision*, *16*(10):1, 1–13, doi:10.1167/16.10.1.

doi: 10.1167/16.10.1 Received February 26, 2016; published August 1, 2016 ISSN 1534-7362

saccades despite a decrease in contrast sensitivity (Castet & Masson, 2000; Castet, Jeanjean, & Masson, 2002). Furthermore, when retinal stimulation during fixation mimics intrasaccadic stimuli, a sensitivity drop between fixation and simulated saccadic conditions is also found, suggesting that the stimulus properties themselves are at least partly responsible for saccadic omission (Mackay, 1970a; Brooks & Fuchs, 1975; Diamond, Ross, & Morrone, 2000; García-Pérez & Peli, 2011; Dorr & Bex, 2013). However, studies that show stronger masking for real than simulated saccades demonstrate that central signals may also play a role in saccadic omission (Bedell & Yang, 2001).

What remains to be determined, however, is the nature of the visual processes inhibiting the smear. One potential candidate is visual masking. Retinal smear could be masked by the pre- and/or postsaccadic image (Matin, Clymer, & Matin, 1972; Breitmeyer & Ganz, 1976; Campbell & Wurtz, 1978; Castet et al., 2002). Visual masking, usually studied during stable eye fixation, is defined by a decrease in sensitivity of a briefly presented target by a spatio-temporally adjacent mask (Breitmeyer & Öğmen, 2006). When we make a saccade in a normal viewing environment, both pre- and postsaccadic images are stable, high contrast and often high frequency images; whereas during the saccade, due to its high speed and the therefore fast slip of the image over the retina, the intrasaccadic image will have a lower contrast, energy, and frequency content. This retinal smear may be masked by the pre- and/or postsaccadic images. Evidence in favor of such masking came from a study in which a vertical bar was presented for different durations starting shortly after the onset of a horizontal saccade (Matin et al., 1972). The bar was seen as smeared when it was presented intrasaccadically, but if the bar stayed on after the saccade, subjects reported seeing only a crisp bar. The prolonged postsaccadic presentation of the bar acted as a backward mask. A later study confirmed this finding in a full-field complex environment in which the experimental room was lit at various times with respect to saccades (Campbell & Wurtz, 1978): subjects perceived a smeared image if the room was lit only during the saccade, and a sharp image if the light was on before the saccade began (forward masking), or remained on after the saccade ended, or both. In the above studies the methods are subjective: The task was to report the presence or perceived length of the intrasaccadic smear. These reports may be unreliable, as subjects know that the visual scene does not appear to be smeared during eye movements in ordinary conditions.

In this study we develop an objective technique to measure saccadic smear, and apply it to examine saccadic omission or the masking of retinal smear, and its relation to visual masking. We conducted three experiments. The first experiment was a validation of the new, objective technique. In the second experiment we investigated the origin (peripheral or central) of saccadic omission by comparing normal to dichoptic presentation. Because spatial proximity between stimulus and mask has been found to be a crucial parameter in classic studies of masking, in the third experiment we varied the spatial proximity of the mask to the intrasaccadic target.

Experiment 1: The masking effect

This experiment aimed to replicate the original saccadic masking effect using a new technique. Previous experiments used subjective categorical judgments (Bedell & Yang, 2001; Matin et al., 1972), asking subjects to decide whether they perceived a discrete dot or an elongated trace. Here, we designed an objective task, asking subjects to locate a gap in the saccadic smear.

We created the smear by turning on an LED either during a saccade, or additionally before and after the saccade. The gap in the smear was produced by briefly dimming the LED at various moments during the saccade (see Figure 2). Because the saccade was always downward, the smear—as projected onto visual space—was directed upwards. If the LED was dimmed near the beginning of the saccade, this dimming should have been perceived as a gap near the bottom of the smear—provided that the smear was visible; if the LED was dimmed near the end of the saccade, the gap should have been perceived near the top of the smear.

The logic behind this localization task was that if observers could not see the smear, they would not be able to localize the gap in the smear. Because we verified that in optimal, no-mask conditions the position of the gap in the smear was clearly visible, the slopes of the psychometric curves in the gap localization task could be used to objectively measure smear visibility.

Methods

Subjects

Seventeen subjects, including the first author, took part in the experiment (mean age: 28.4 years, *SD* 4; six men, 11 women). All signed a consent form in agreement with the Declaration of Helsinki, received financial compensation (10€/hr), had normal or corrected-to-normal vision, and were naïve regarding the purpose of the experiment (except the first author). Most (14/17) were experienced psychophysical observers.

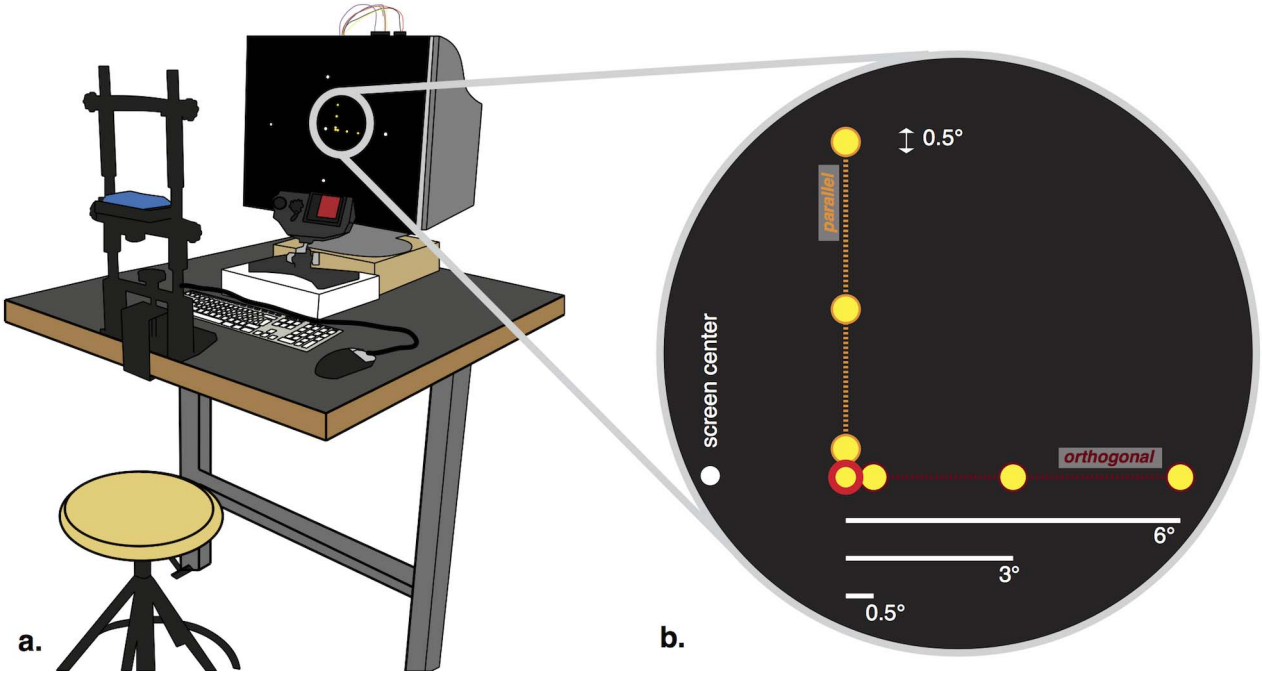

Figure 1. (a) Setup of the experiment. (b) Close-up view of the center of the cardboard figuring the screen center and the different LEDs used. The LED surrounded by red is the one used for Experiments 1 and 2. All LEDs were used only in Experiment 3. Dashed lines indicate the axes of the masking LEDs used in Experiment 3 with respect to the axis of the saccade.

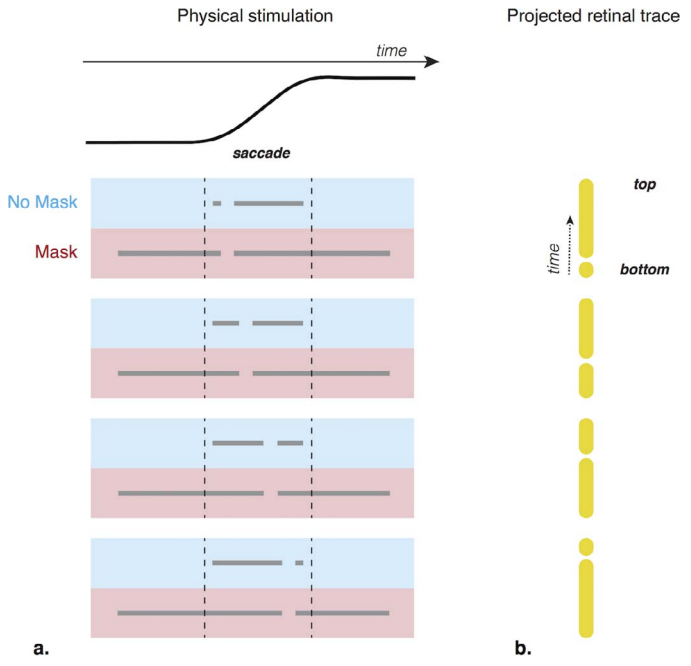

Figure 2. (a) Time course of the presentation of the LED with respect to the saccade in the two masking conditions. At the top of the panel, the gap occurs at the beginning of a saccade and at the bottom of the panel it occurs at the end. (b) Corresponding projection into the visual field of the retinal trace in the case of a vertical downward saccade. For example, the top panel is the projected retinal trace that corresponds to a gap at the beginning of the saccade.

Apparatus

Subjects were seated so that the eye was at an approximate distance of 57.3 cm from the computer monitor (Sony GDM F520), centered at eye level. A chin and head rest were used to stabilize the head while eye movements were tracked using an EyeLink 1000 video eyetracker (SR Research Ltd., Mississauga, Ontario, Canada) with a 35 mm lens and operating at a sampling rate of 1000 Hz. The experiment was controlled by a PC, which received real-time data from the eyetracker (no link filter, 1 ms of delay) and controlled the displays—on the monitor and the LED. The LED was controlled by a dedicated program running on an Arduino Due microcontroller board (http://arduino.cc), communicating with the PC using the USB serial port (set so that there was a 1 ms maximum measured delay between the PC command and change in luminosity). The LED was mounted on black cardboard positioned directly in front of the monitor, parts of which were visible through holes cut in the cardboard (see Figure 1a). The room was dimly lit in order to attenuate potentially disturbing aftereffects caused by the stimuli.

Stimuli

The main stimulus was an LED (0.5° diameter, 2 mcd, CIE $x = 0.544$, $y = 0.455$) mounted on black cardboard in front of the computer monitor, 3° to the

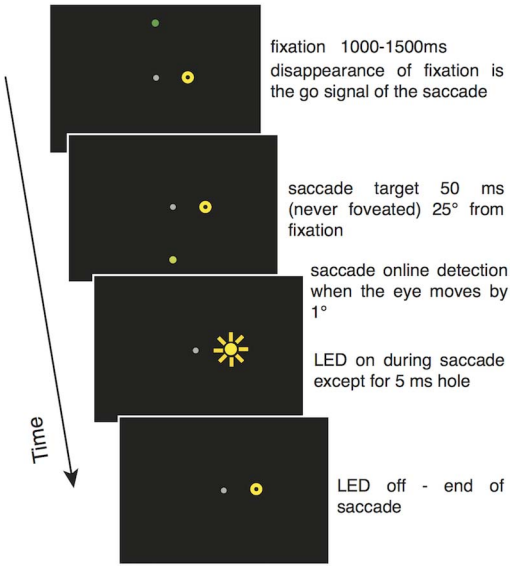

Figure 3. Time course of a No Mask trial. The gray dot indicates the (invisible) position of the screen center. The LED was located at 3° to the right of the vertical line connecting fixation and saccade target.

right of monitor center (Figure 1b). Through holes in the cardboard subjects could also see two green disks (0.5° diameter) displayed on the monitor, positioned so that one was directly above the other, with a vertical separation of 25°. These disks were used as fixation and saccade targets.

The LED was turned on either only during the saccade (No Mask condition), or additionally before and after the saccade (Mask condition)—see Figure 2. In all conditions, at some point during the saccade, the LED intensity was decreased to 0 using an inverted cosine function then back to maximum intensity. This "gap" in the stimulus lasted 5 ms.

Temporally the gap was presented centered at 20%, 40%, 60%, or 80% of the total estimated saccade duration. Saccade duration was measured individually in a pretest in which subjects performed 50 saccades between the same targets as in the main experiment. Mean saccade duration and mean delay between actual saccade onset and online saccade detection were computed offline after the pretest in order to adjust the timing of the gap.

If subjects could perceive the saccadic smear corresponding to this stimulus, the gap would be seen at different positions; for example, a gap near the beginning of a downward saccade would be seen at the bottom of the perceived smear (Figure 2).

Procedure

On each trial, a green disk appeared at the top of the monitor and when it disappeared, subjects were to saccade to the green disk briefly flashed for 50 ms at the bottom. The two disks were at the same location on every trial (Figure 3). Subjects were asked to report whether the gap in the LED smear was at the top or at the bottom of the smear by rolling the mouse wheel up or down. They were also instructed not to always use the same response button if they did not see a gap or could not localize it.

The LED was presented in one of two conditions: a No Mask condition (example Figure 3) in which the LED was on only during the saccade, and a Mask condition in which the LED was on before (forward mask), during (as in the No Mask condition) and after (backward mask) the saccade (Figure 2). In the Mask condition, the LED was turned on simultaneously with the go signal (such that the duration of the forward mask was equal to saccade latency) and was extinguished approximately 300 ms after the predicted end of the saccade (Supplementary Material S1).

At the start of the experiment, after performing the pretest to measure saccade durations, subjects familiarized themselves with the task for as long as they wished (on average, subjects ran 95 familiarization trials). After the familiarization phase, subjects began the main experiment, which consisted of 400 trials divided into five blocks of 80 trials. Each of the four gap positions was tested 50 times in each condition. The experiment took approximately an hour.

Data analysis

Eye movement analysis

Saccade extraction: Eye position data were filtered with a 40 ms moving average window. We defined saccade onset as the first of five successive samples (at 1000 Hz) above a speed threshold of 30°/s and its offset as the first subsequent sample below this threshold. In order to partly correct for the time delays introduced by the moving average, we subtracted 20% of the duration of the moving window (8 ms) from saccade start and end times (Supplementary Figure S2).

Saccade selection: In the following analyses we included only trials in which the saccade began 100 to 600 ms after the go signal (fixation point offset) and had a minimum amplitude of 60% of saccade amplitude and for which no missing samples between the go signal and the end of the saccade were found. Twelve percent of the trials were excluded from the analyses because the saccade did not fit these criteria.

Offline computation of the position of the gap

The exact position of the gap with respect to the retinal extent of the smear was computed offline. This position depended on the time at which the LED was

dimmed (20%–80% of the estimated mean saccade duration) and the time course and amplitude of the actual saccade. The position of the gap was expressed with respect to the smear, so that 0 corresponded to the bottom of the smear, 0.5 to the spatial center of the smear, and 1 to the top. On a small fraction of the trials (2%), the saccade was briefer than expected, and the gap occurred after the end of the saccade. These trials were discarded.

Psychometric curve fits

Perceptual responses as a function of gap position were fitted by a logistic function, $R(x) = 1/[1 + e^{-k(x-x_0)}]$, where x_0 is the position at which the gap appears centered on the smear, and k the slope of the psychometric curve, measuring the precision of the position judgment. These parameters were estimated using maximum likelihood with a prior on x_0, $P(x_0) = 1 / \{1 + [(x_0 - 0.5) / w]^p\}$, with $w = 0.475$ and $p = 50$, that strongly favors values of x_0 that lie inside the smear. We estimated confidence intervals by using the bootstrap with 2,500 iterations for each condition in each subject and for the overall mean. We performed paired sample t tests on the slopes of the psychometric functions to assess differences in performance between the two conditions.

Results

Mean saccade latency was 200 ms (SD ±28 ms), duration was 97 ms (±23 ms) and amplitude was 24.2° (±3°). Recall that the duration of the forward mask was equal to saccade latency. Mean duration of the backward mask was 273 ms (±19 ms). Average saccadic speed at the presentation of the gap was 296°/s (±66°/s), corresponding to a spatial gap of 1.5° (±0.3°).

Performance was significantly better in the No Mask condition (mean slope of 4.34) than in the Mask condition (mean slope of 0.32) at the group level: The slopes of the psychometric functions were significantly higher in the No Mask condition than in the Mask condition ($t_{16} = 6.15$, $p < 0.001$, $\eta^2 = 0.70$). Moreover, the slopes in the Mask condition were not significantly different from 0 (95% CI[–0.48, 1.23]). Individually, the fitted slope was higher in the Mask than in the No Mask condition in all 17 subjects, and this difference reached significance in 10 out of 17 (Figure 4).

Subjects were significantly better in locating the position of the gap in the No Mask condition than in the Mask condition. Thus, in the case of a solely intrasaccadic stimulation, it is easy to perceive the smear (and therefore the gap in it), but if the LED is already on before the beginning of the saccade and stays on after the end, performance drops drastically. The retinal smear itself during the saccade is the same in the two conditions, so the presence of the LED before or after the saccade therefore acts as a forward and/or backward mask on the intrasaccadic stimulus. Experiment 1 demonstrated that perisaccadic stimuli mask the saccadic smear (Matin et al., 1972; Bedell & Yang, 2001), but did so using an objective technique, showing that in the presence of the perisaccadic masks, subjects are unable to localize the gap in the smear. In Experiment 2 we questioned the origin of the interactions between mask and target that achieve masking.

Experiment 2: Peripheral or central origin?

Saccades rapidly change the low-level luminance and contrast characteristics of the proximal visual signal. Therefore we can postulate that some peripheral mechanisms of adaptation might be involved in saccadic omission; and it has been proposed that low-level mechanisms, like contrast gain modulation—a mechanism already present in the retina (Shapley & Victor, 1981; Benardete, Kaplan, & Knight, 1992)—might be involved in saccadic omission (Burr & Morrone, 1996; Gu, Hu, Li, & Hu, 2014). Studies of contrast masking during fixation using dichoptic presentation showed that masking was reduced by presenting the mask and target to different eyes and that the contrast adaptation level of one eye determines sensitivity only for that eye (Battersby & Wagman, 1962; Blake, Breitmeyer, & Green, 1980; Chubb, Sperling, & Solomon, 1989). Other studies propose that mechanisms at a later, cortical, stage underlie target-mask interactions around saccades, as is the case for metacontrast masking that survives dichoptic presentation (Kolers & Rosner, 1960; Schiller & Smith, 1968; Weisstein, 1971).

Here we investigated the locus of origin of saccadic smear masking by comparing performance in normal viewing to dichoptic presentation. A decrease of masking in the dichoptic viewing condition would suggest that the masking of saccadic smear by pre- or postsaccadic stimuli has a partly precortical component (Macknik & Martinez-Conde, 2004). In Experiment 2 we presented both No Mask and Mask condition in binocular and dichoptic viewing conditions in the same session, with subjects who had never seen the stimulus before.

Methods

Subjects

Twelve subjects took part in the experiment. However, three of them took part in a preliminary phase but failed

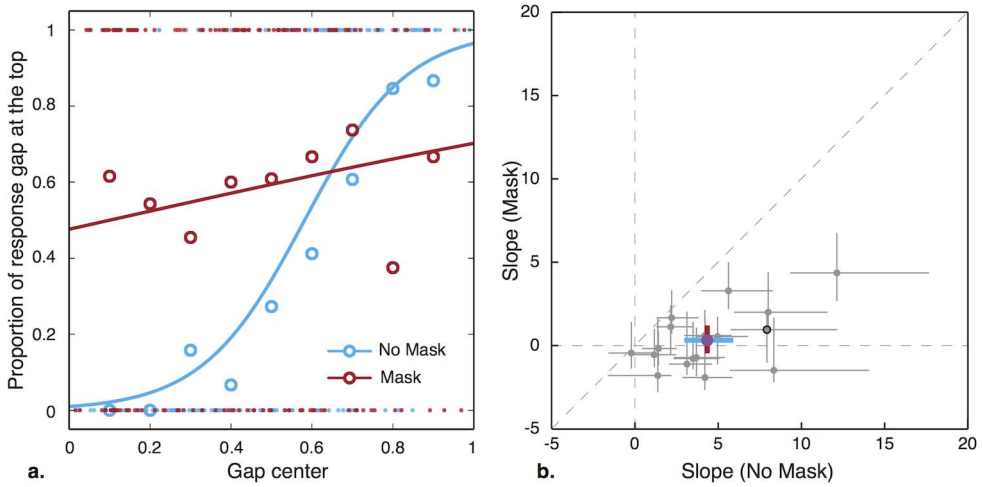

Figure 4. (a) Example of data and psychometric fits for one participant. The proportion of response gap at the top of the smear is plotted against the position of the gap with respect to the length of the smear (0 is the beginning of the smear seen at the bottom, and 1 is the end of the smear seen at the top). Both binned data (circles) and raw data (filled dots at the top and the bottom of the graph) are displayed. This subject had a slope of 7.9 in the No Mask condition (corresponding to a JND of 0.14, meaning that a change in the position of the gap by 14% of the smear length was enough to elicit a reliable discrimination between a gap perceived at the top and a gap perceived at the bottom of the smear) and a slope of 1.0 in the Mask condition (corresponding JND of 1.2). (b) The slopes of the psychometric curves in the Mask condition are plotted against the slopes in the No Mask conditions for all subjects. Error bars indicate the 95% confidence intervals obtained by bootstrap. The colored cross represents means and their confidence intervals. The data point corresponding to the example participant in (a) is outlined in black.

to meet the criteria to take part to the main experiment (see below). Thus, nine subjects were included in the analyses (mean age 26.8 years, *SD* 6.6; one man, eight women). Because of technical constraints, subjects wearing either glasses or contact lenses did not participate. Thus, all had normal vision without correction and none had seen the stimuli before the experiment.

Apparatus

The apparatus was identical to Experiment 1 except that subjects wore shutter glasses (Plato glasses, Translucent Technologies, Toronto, Canada) during the entire experiment. When open, these shutter glasses transmit about 80% of the visible light; when closed, they are translucent (i.e., transmit light but not images) rather than opaque. The two sides of the glasses were independently controlled online by the Arduino microcontroller (delay between command and execution is 4 ms to open and 3 ms to close the glass). We set the EyeLink eyetracker to binocular recording mode and used the corresponding 25 mm lens; filtering level was set to standard (2-ms delay). Because of the physical constraints of the shutter glasses, we had to remove the head rest (but not the chin rest).

Stimuli

Stimuli were identical to those in Experiment 1 (but with luminance attenuated by 20%). However, in the dichoptic trials, by switching the open and closed lenses of the shutter glasses, the intrasaccadic stimulus was presented to one eye whereas pre- and postsaccadic stimuli were presented to the other eye.

Procedure

The session started with a training phase that included only the No Mask condition in normal viewing (subjects wore the shutter glasses with both lenses open). Indeed, the first experiment demonstrated the effect of masking, but in the present experiment we wanted to maximize the chance of finding an interaction between viewing and masking conditions, so we wanted subjects with high performance in the No Mask condition. This training phase consisted of blocks of 80 trials (20 repetitions of four gap positions). Subjects were allowed to continue to the main experiment as soon as their mean fraction of "correct" responses on a block exceeded 60%. (A "correct" response was defined as responding "bottom" for the 20% and 40% gap positions, and "top" for 60% and 80%.) Three subjects did not meet this criterion after three blocks.

In the main experiment, the masking conditions (No Mask and Mask) and instructions were identical to Experiment 1. The only difference was the use of shutter glasses and the addition of dichoptic presentation. The presence of a dichoptic No Mask condition might seem contradictory because we present nothing to one eye and the smear to the other—which is very

similar to the normal viewing No Mask condition. However, it is necessary as a no-mask equivalent to the dichoptic Mask condition (to equate for shutter glasses switching sides and monocular viewing of the smear). The dichoptic trials began with the presentation of the fixation target at the top, which subjects could view with only one eye (e.g., the left eye). They were to saccade to the briefly flashed target at the bottom when the fixation target disappeared. The viewing eye switched as soon as the eye moved 1° from fixation (e.g., the left lens closed and the right lens opened). The online criterion for the end of a saccade was eye speed falling below 30°/s for three successive samples. When this criterion was reached, the viewing eye switched back (e.g., right lens closed and left lens opened). Subjects were also told that the two sides of the glasses would open and close during a trial, which would be disturbing at first, but they should try not to pay attention to it and focus on the stimuli and the task. The main experiment consisted of 640 trials divided into eight blocks of 80 trials. Each of the four gap positions was tested 40 times in the two masking conditions and in the two viewing conditions. Instructions and response mode were identical to the previous experiment. The entire session took approximately 2 hrs.

Data analysis

The same criteria as in Experiment 1 were applied to select valid trials. Because of the shutter glasses, eye-tracking data were noisier and 26% of trials were excluded.

We wanted to compare performance in the No Mask and Mask conditions for both dichoptic viewing and normal viewing. We therefore conducted repeated-measures ANOVA on the slopes of the psychometric functions of all subjects with two factors: viewing (normal and dichoptic) and masking (No Mask and Mask).

Results

Mean saccade duration was 93 ms (*SD* ±8 ms), amplitude was 21° (±2.3°), and latency (forward mask) was 217 ms (±18 ms). Mean backward mask duration was 275 ms (±9 ms). Average saccadic speed at the presentation of the gap was 275°/s (±34°/s), corresponding to a spatial gap of 1.4° (±0.2°).

Results are displayed Figure 5. The ANOVA showed a main effect of masking , $F(1, 8) = 33.6$, $p < 0.001$, $\eta^2 = 0.81$, but no effect of viewing, $F(1, 8) = 1.22$, $p = 0.3$, and no significant interaction between viewing and masking conditions, $F(1, 8) = 3.03$, $p = 0.12$, with Bayes factor $BF_{01} = 2.4$, which constitutes a weak evidence in favor of the null hypothesis of no interaction between viewing and masking condition. Again, this means that

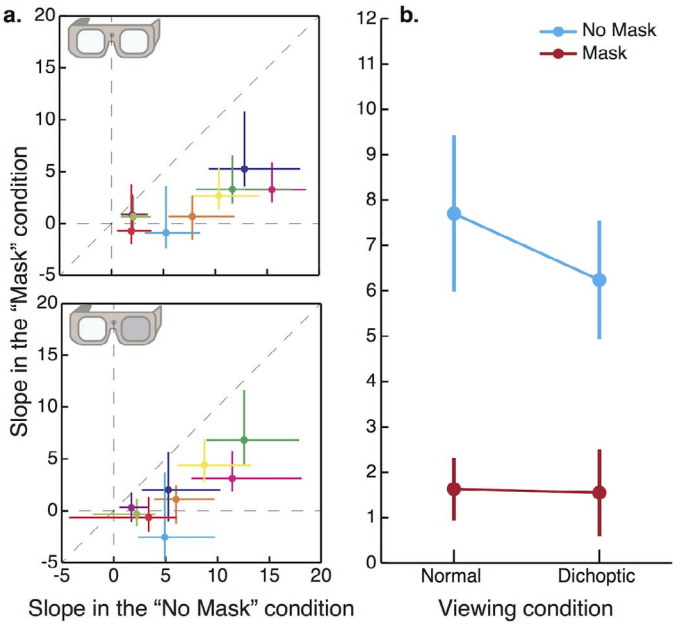

Figure 5. (a) Individual data in the normal viewing conditions for the upper panel and in the dichoptic viewing condition in the lower panel. (b) Average slopes across participants. Error bars represent standard errors of the mean.

performance decreased in the Mask condition, but that dichoptic viewing did not modify the effect of the mask. Thus, we have no evidence that a dichoptically presented mask is any less efficient than a mask presented to the same eye in masking saccadic smear.

It should be pointed out that when one eye is covered, its direction deviates slightly from that of the open eye, an effect known as heterophoria. Thus, the smear and the mask in the dichoptic condition may have been slightly misaligned. However, median heterophoria in healthy subjects for near viewing is rather small, with typical values having been reported as 0.3° (Saladin & Sheedy, 1978) or 1.7° (Morgan, 1944), so the misalignment was most likely very small. As will be shown in Experiment 3, below, even larger values of smear-mask misalignment have no systematic effect on masking.

Those results suggest that interactions between masks (pre- and postsaccadic images) and target (smear) take place centrally, after the side of binocular convergence. Our next step was to investigate the spatial specificity of saccadic omission.

Experiment 3: Spatial extent of the masking

Visual masking usually depends strongly on the spatial distance between mask and target. The classic

task involves a disk (the target) surrounded by an annulus (the mask), and as the separation between target and mask increases, masking decreases (Kolers & Rosner, 1960; Growney, Weisstein, & Cox, 1977; Breitmeyer & Horman, 1981; Breitmeyer, Rudd, & Dunn, 1981). In these studies, stimuli are presented during fixation and therefore spatial distance is also retinal distance. In the case of a saccade, however, if pre- and postsaccadic masks are at the same spatial location as the intrasaccadic stimulus, they occupy different retinal locations. In Experiment 3 we tested whether masking of the saccadic smear depended on the spatial and retinal proximity between mask and target.

Methods

Subjects

Eleven subjects (mean age 30 years, *SD* 3.8; four men, seven women) including the first author took part in this study. All had previously participated in Experiment 1. The data of two additional subjects were not included in the analysis because in the No Mask condition, the slope of their psychometric function was not significantly different from 0.

Stimuli

Stimuli were identical to those of Experiment 1, except that we added additional masking conditions. Thus, on every trial, the intrasaccadic stimulus included a gap inserted at 20%, 40%, 60%, and 80% of the saccade duration estimated as in Experiment 1. The same LED always generated this intrasaccadic stimulus (Figure 1b). In addition to a No Mask condition in which only this intrasaccadic stimulus was presented at saccade onset detection (a replication of Experiments 1 and 2), we had 5 other masking conditions, differing by the spatial distance between the LED generating the intrasaccadic stimulus and the masking LED. The masking LED could be the same as the target (0° distance—a replication of Experiments 1 and 2), adjacent to the LED (0.5° distance) or at 3° of eccentricity from the LED on axes parallel and orthogonal to the saccade (see Figure 1b). A subset of six subjects also runs one additional distance condition at 6° of eccentricity on both axes.

Procedure

The masking LED was turned on at the go signal and was turned off either at 200 ms (mean saccade latency in Experiment 1) or at saccade onset detection if it occurred before 200 ms—acting as a forward mask. This LED was turned back on for 300 ms at the predicted end of the saccade—acting as a backward mask. Subjects were told that the stimulus that contained the gap would always be at the same location among trials and identical to the one in the previous experiment. They were also told that they would see distractors at other locations that they should ignore and focus on perceiving the gap position. Subjects who ran six conditions performed a total of 960 trials, 40 repetitions of four gap positions for each condition. Subjects who ran eight conditions performed a total of 1,280 trials divided in four sessions of 320 trials. The experiment lasted approximately 2 hrs.

Data analysis

Eye movement analysis, offline computation of the smear and fit of the responses were performed in the same way as in Experiment 1. We additionally removed trials for which the backward mask started before the end of the saccade and lasted more than 20% of the saccade amplitude, because it might interfere with the task. We excluded 22% of trials.

We then applied the same two analyses to both the whole sample of 11 subjects and the subset of six subjects. First we performed repeated-measures ANOVA on the slopes of the psychometric functions with one factor condition (six masking modalities for the 11 subjects: No Mask, 0, Para-0.5, Para-3, Ortho-0.5, Ortho-3; and eight for the subset of six subjects who ran Para-6 and Ortho-6; "Para" and "Ortho" referring to masks that were on the axis parallel or orthogonal to the saccade as illustrated in Figure 1b) and the following pairwise comparisons with a Bonferroni correction for multiple comparisons. We applied a Greenhouse-Geisser correction when the assumption of sphericity was violated. Secondly, a repeated-measures ANOVA was carried out considering only the masking conditions to find out if there was any effect of the distance (three modalities for the whole sample: 0°, 0.5°, 3°; and four for the subset including a distance of 6°) and the direction with respect to the saccade of the masks (two modalities: Parallel, Orthogonal in both groups).

Results

Mean saccade latency was 194 ms (*SD* ±15 ms), duration was 95 ms (±17 ms), and amplitude was 25° (±3.8°). Mean duration of the backward mask was 288 ms (±10 ms). Average saccadic speed at the presentation of the gap was 306°/s (±57°/s), corresponding to a spatial gap of 1.5° (±0.3°).

Results are presented in Figure 6. There was a main effect of the condition for both the whole sample,

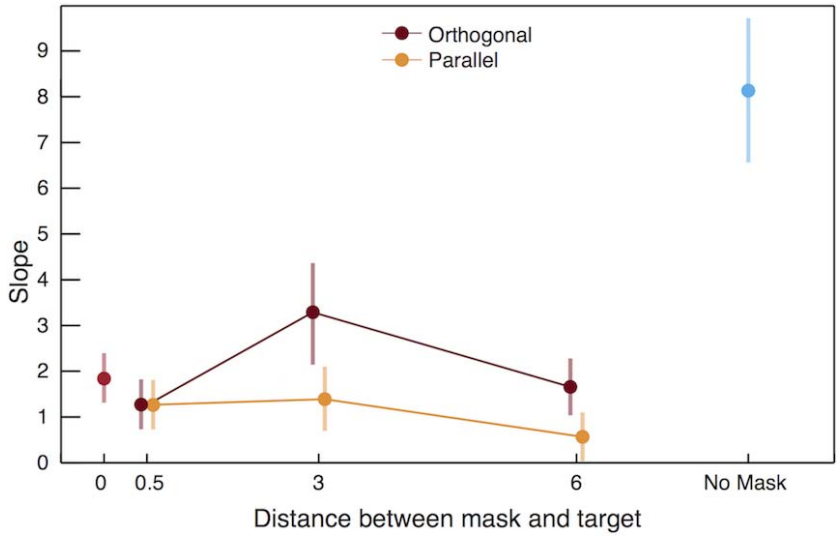

Figure 6. Average slopes of the psychometric curves for all conditions. Error bars represent standard errors of the mean. Six subjects for 6° distances between mask and target and 11 for all other conditions.

$F(1.51, 15.07) = 18.02$, $p < 0.001$, $\eta^2 = 0.64$, and the subset, $F(2.1, 10.3) = 5.13$, $p = 0.028$, $\eta^2 = 0.51$. In the whole sample, the only significant pairwise comparisons indicated that performance was better in the No Mask condition than in all the other conditions (for all those pairs, $p < 0.05$). However in the subset of six subjects, no pairwise comparisons were significant.

Performance was not significantly different with increasing distance between mask and target for the whole sample, $F(2, 20) = 2.58$, $p = 0.1$, or for the subset, $F(3, 15) = 1.12$, $p = 0.37$. And there was no main effect of the axis with respect to the saccade for the whole sample, $F(1, 10) = 3.49$, $p = 0.09$, or for the subset, $F(1, 5) = 1.16$, $p = 0.33$. These results suggest that saccadic smear masking survives separations of as much as 6°.

Discussion

Here we have investigated the conditions that lead to saccadic omission, or, on the contrary, allow the intrasaccadic smear to be perceived. In past work, the perception of the intrasaccadic smear was evaluated using subjective reports (Matin et al., 1972; Campbell & Wurtz, 1978). Here we used an objective performance criterion: We punched a gap in the smear by very briefly dimming the stimulus during the saccade. We reasoned that features of the gap such as its location in space would be visible to the extent that the overall smear is itself visible. We therefore evaluated smear visibility indirectly, as the slope of the psychometric curve in localizing the gap.

In a first experiment we validated our technique by comparing a condition in which an LED target was lit only during a saccade, leading to a smear on the retina, to a condition in which the target was additionally lit for several hundred milliseconds before and after the saccade (we will refer to the pre- and postsaccadic target as the "mask"). We found that the slopes of the psychometric curves were significantly decreased by the pre- and postsaccadic mask. Thus we replicated the results on perisaccadic smear masking (Matin et al., 1972; Campbell & Wurtz, 1978) using our objective technique. Thus, we have shown that smear is much more visible without pre- and postsaccadic masks than when the masks are present. We should point out that the perceived smear differs in its geometry from the smear on the retina: The perceived smear is about half as long as the projection of the retinal smear, typically starting near the end (Hershberger, 1987; Watanabe, Noritake, Maeda, Tachi, & Nishida, 2005).

In the second experiment we investigated the origin of saccadic omission by comparing monocular to dichoptic presentation of the smear and masks. If masking is peripheral in origin, then dichoptic masking should be weaker than monocular; if, on the contrary, dichoptic masking is as strong as monocular, then the origin of masking is located at or after the locus of binocular convergence in the cortex. We found that masking was as strong when masks and target were presented to different eyes than when they were presented to the same eye. It interesting to note that Mackay found a dichoptic decrease of sensitivity of intrasaccadic targets with simulated saccades if the intrasaccadic target was presented to one eye and the moving background to the other eye

(Mackay, 1970b). We didn't find any evidence in favor of the involvement of peripheral mechanisms to account for intrasaccadic smear masking. Although it is highly probable that low-level, peripheral adaptation also takes place around saccades, a cascade of adaptation reactions takes place at many levels of the visual hierarchy (Dhruv & Carandini, 2014). Our results seem to indicate that central cortical mechanisms play a crucial role in masking the saccadic smear.

In the third experiment we varied spatial proximity between mask and target and found that smear masking was as strong when mask and target were separated by as much as 6° as when they coincided spatially. Studies of visual masking that vary spatial proximity between mask and target often find a decrease in masking with spatial separation (Kolers & Rosner, 1960; Growney et al., 1977; Breitmeyer & Horman, 1981; Breitmeyer, Rudd, & Dunn, 1981). However, the fall-off in masking strongly depends on stimulus size, eccentricity, and task, and masking can still occur with large spatial separations (Growney et al., 1977; Hein & Moore, 2010). Note that in our experiment eccentricity of the masked stimulus was 3°. There could nonetheless be an effect of proximity that our paradigm is not sensitive enough to detect, or the fall-off in masking could occur for separations above 6°. Nevertheless, our results still show that even if there were a fall-off with larger separations, it is not crucial to account for our lack of perception of the smear. Low-level characteristics of natural images have wide distributions (Mante, Frazor, Bonin, Geisler, & Carandini, 2005; Frazor & Geisler, 2006) and these characteristics can change drastically from one fixation to the next. Therefore, to achieve masking of the smear, it would make sense to assume that the visual system takes into account characteristics of a large part of the visual scene. Such contextual effects could be subtended by extraclassic receptive fields (Allman, Miezin, & McGuinness, 1985; Seriès, Lorenceau, & Frégnac, 2003).

In this study we did not explore stimulus parameters that could have made the smear more or less visible, namely the luminance of the LED or smear itself, and the luminance of the background. Nor did we explore the task parameter of gap size that could globally increase or decrease performance. The fact that we used fixed parameter values, rather than individually computed thresholds, likely accounts for the large individual differences in overall performance found in all three experiments, including the several subjects that had shallow slopes even in the absence of masking.

It is likely that ordinary visual masking during fixation and masking of the saccadic smear share some common mechanisms because of several functional similarities. One similarity concerns the duration of stimuli that can be masked (Breitmeyer & Öğmen, 2006), which is close to the typical durations of saccades (Baloh, Sills, Kumley, & Honrubia, 1975; Carpenter, 1988). Another similarity is that while we are usually unaware of the intrasaccadic image, it can still be processed by the visual system (Cameron, Enns, Franks, & Chua, 2009; Castet et al., 2002). This is also the case with ordinary masking, as demonstrated by masked priming (e.g., Dehaene & Naccache, 2001). Visual masking refers to a large ensemble of separate phenomena and underlying mechanisms (Breitmeyer & Öğmen, 2006)—which may very well include intrasaccadic smear masking.

We have been assuming that the origin of smear masking is visual. However, others have argued that the suppression of the intrasaccadic percept requires an extraretinal signal arising from the eye movement (Bedell & Yang, 2001; Bedell, Tong, & Aydin, 2010). Although an extraretinal signal may be involved, it should be noted that its presence in the no-mask condition is not sufficient to suppress the smear. What does mask the smear is an additional visual signal, the pre- and postsaccadic masks. In order to test the role of extraretinal efference copy, one has to compare the effect of pre- and postsaccadic masks on smear perception during real saccades and simulated saccades, obtained by moving the target on a saccadic trajectory while the subject fixates. Bedell and Yang (2001) ran a similar experiment with a subjective task in which subjects reported perceived smear length, and found contributions of both visual masking and efference copy. Thus, saccadic omission under real-world conditions may rely on both types of mechanisms.

Finally, we should point out that our stimuli differ significantly from ones in ecological settings. Perhaps the biggest difference concerns overlap. In the case of our point-light stimuli, the smear and the clear pre- and postsaccadic images touch but do not overlap. In real settings, each time we saccade the entire retina is covered by pre and postsaccadic masks, which also cover the intrasaccadic smear. Whereas our simple point-light stimuli are based on those used by Matin et al. (1972), Campbell and Wurtz (1978) discovered similar effects of pre- and postsaccadic masks on smear suppression for complex, large-field stimuli. Although this increases our confidence that our findings will generalize to real-world environments, it would be worthwhile to develop an analogous objective methodology for probing saccadic omission with large-field stimuli. Armed with such a methodology, it would be interesting to study whether the postsaccadic image has to be identical to the presaccadic one for smear masking to occur.

Keywords: vision, saccades, masking, saccadic smear

Acknowledgments

This work was supported by a doctoral fellowship from the Direction Générale de l'Armement (France) to MD, and by a European Research Council grant (agreement n°AG324070).

Commercial relationships: none.
Corresponding author: Marianne Duyck.
Email: marianne.duyck@gmail.com.
Address: Laboratoire Psychologie de la Perception (Université Paris Descartes & CNRS - UMR 8242), 45, rue des Saints-Pères, Paris, France.

References

Allman, J., Miezin, F., & McGuinness, E. (1985). Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local-global comparisons in visual neurons. *Annual Review of Neuroscience*, *8*(1), 407–430, doi.org/10.1146/annurev.ne.08.030185.002203.

Baloh, R. W., Sills, A. W., Kumley, W. E., & Honrubia, V. (1975). Quantitative measurement of saccade amplitude, duration, and velocity. *Neurology*, *25*(11), 1065–1065, doi.org/10.1212/WNL.25.11.1065.

Barlow, H. B. (1958). Temporal and spatial summation in human vision at different background intensities. *The Journal of Physiology*, *141*(2), 337–350, doi.org/10.1113/jphysiol.1958.sp005978.

Battersby, W. S., & Wagman, I. H. (1962). Neural limitations of visual excitability. IV: Spatial determinants of retrochiasmal interaction. *American Journal of Physiology—Legacy Content*, *203*(2), 359–365.

Bedell, H. E., Tong, J., & Aydin, M. (2010). The perception of motion smear during eye and head movements. *Vision Research*, *50*(24), 2692–2701, doi.org/10.1016/j.visres.2010.09.025.

Bedell, H. E., & Yang, J. (2001). The attenuation of perceived image smear during saccades. *Vision Research*, *41*(4), 521–528, doi.org/10.1016/S0042-6989(00)00266-2.

Benardete, E. A., Kaplan, E., & Knight, B. W. (1992). Contrast gain control in the primate retina: P cells are not X-like, some M cells are. *Visual Neuroscience*, *8*(05), 483–486, doi.org/10.1017/S0952523800004995.

Blake, R., Breitmeyer, B. G., & Green, M. (1980). Contrast sensitivity and binocular brightness: Dioptic and dichoptic luminance conditions. *Perception & Psychophysics*, *27*(2), 180–181, doi.org/10.3758/BF03204308.

Breitmeyer, B. G., & Öğmen, H. (2006). *Visual masking: Time slices through conscious and unconscious vision*. Oxford, UK: Oxford University Press.

Breitmeyer, B. G., & Ganz, L. (1976). Implications of sustained and transient channels for theories of visual pattern masking, saccadic suppression, and information processing. *Psychological Review*, *83*(1), 1–36, doi.org/10.1037/0033-295X.83.1.1.

Breitmeyer, B. G., & Horman, K. (1981). On the role of stroboscopic motion in metacontrast. *Bulletin of the Psychonomic Society*, *17*(1), 29–32, doi.org/10.3758/BF03333658.

Breitmeyer, B. G., Rudd, M., & Dunn, K. (1981). Metacontrast investigations of sustained–transient channel inhibitory interactions. *Journal of Experimental Psychology: Human Perception and Performance*, *7*(4), 770–779, doi.org/10.1037/0096-1523.7.4.770.

Brooks, B. A., & Fuchs, A. F. (1975). Influence of stimulus parameters on visual sensitivity during saccadic eye movement. *Vision Research*, *15*(12), 1389–1398.

Burr, D. C., & Morrone, M. C. (1996). Temporal impulse response functions for luminance and colour during saccades. *Vision Research*, *36*(14), 2069–2078, doi.org/10.1016/0042-6989(95)00282-0.

Burr, D. C., Morrone, M. C., & Ross, J. (1994). Selective suppression of the magnocellular visual pathway during saccadic eye movements. *Nature*, *371*(6497), 511–513, doi.org/10.1038/371511a0.

Burr, D. C., & Ross, J. (1982). Contrast sensitivity at high velocities. *Vision Research*, *22*(4), 479–484, doi.org/10.1016/0042-6989(82)90196-1.

Cameron, B. D., Enns, J. T., Franks, I. M., & Chua, R. (2009). The hand's automatic pilot can update visual information while the eye is in motion. *Experimental Brain Research*, *195*(3), 445–454, doi.org/10.1007/s00221-009-1812-7.

Campbell, F. W., & Wurtz, R. H. (1978). Saccadic omission: Why we do not see a grey-out during a saccadic eye movement. *Vision Research*, *18*(10), 1297–1303, doi.org/10.1016/0042-6989(78)90219-5.

Carpenter, R. H. S. (1988). *Movements of the eyes* (2nd ed.). London, UK: Pion Ltd.

Castet, E. (2010). Perception of intra-saccadic motion. In G. S. Masson & U. J. Ilg (Eds.), *Dynamics of*

visual motion processing: Neuronal, behavioral, and computational Approaches (pp. 213–235). New York: Springer.

Castet, E., Jeanjean, S., & Masson, G. S. (2002). Motion perception of saccade-induced retinal translation. *Proceedings of the National Academy of Sciences, USA, 99*(23), 15159–15163, doi.org/10.1073/pnas.232377199.

Castet, E., & Masson, G. S. (2000). Motion perception during saccadic eye movements. *Nature Neuroscience*, *3*(2), 177–183, doi.org/10.1038/72124.

Chubb, C., Sperling, G., & Solomon, J. A. (1989). Texture interactions determine perceived contrast. *Proceedings of the National Academy of Sciences, USA, 86*(23), 9631–9635.

Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition*, *79*(1-2), 1–37.

Dhruv, N. T., & Carandini, M. (2014). Cascaded effects of spatial adaptation in the early visual system. *Neuron*, *81*(3), 529–535, doi.org/10.1016/j.neuron.2013.11.025.

Diamond, M. R., Ross, J., & Morrone, M. C. (2000). Extraretinal control of saccadic suppression. *The Journal of Neuroscience*, *20*(9), 3449–3455.

Dorr, M., & Bex, P. J. (2013). Peri-saccadic natural vision. *The Journal of Neuroscience*, *33*(3), 1211–1217, doi.org/10.1523/JNEUROSCI.4344-12.2013.

Frazor, R. A., & Geisler, W. S. (2006). Local luminance and contrast in natural images. *Vision Research*, *46*(10), 1585–1598, doi.org/10.1016/j.visres.2005.06.038.

García-Pérez, M. A., & Peli, E. (2011). Visual contrast processing is largely unaltered during saccades. *Frontiers in Psychology*, *2*, 247, doi.org/10.3389/fpsyg.2011.00247.

Growney, R., Weisstein, N., & Cox, S. I. (1977). Metacontrast as a function of spatial separation with narrow line targets and masks. *Vision Research*, *17*(10), 1205–1210, doi.org/10.1016/0042-6989(77)90155-9.

Gu, X.-J., Hu, M., Li, B., & Hu, X.-T. (2014). The role of contrast adaptation in saccadic suppression in humans. *PLoS ONE*, *9*(1), e86542, doi.org/10.1371/journal.pone.0086542.

Hein, E., & Moore, C. M. (2010). Unmasking the standing wave of invisibility: An account in terms of object-mediated representational updating. *Attention, Perception & Psychophysics*, *72*(2), 398–408, doi.org/10.3758/APP.72.2.398.

Hershberger, W. (1987). Saccadic eye movements and the perception of visual direction. *Perception & Psychophysics*, *41*(1), 35–44, doi.org/10.3758/BF03208211.

Higgins, E., & Rayner, K. (2014). Transsaccadic processing: Stability, integration, and the potential role of remapping. *Attention, Perception, & Psychophysics*, *77*(1), 3–27, doi.org/10.3758/s13414-014-0751-y.

Kolers, P. A., & Rosner, B. S. (1960). On visual masking (metacontrast): Dichoptic observation. *The American Journal of Psychology*, *73*(1), 2–21, doi.org/10.2307/1419113.

Mackay, D. M. (1970a). Elevation of visual threshold by displacement of retinal image. *Nature*, *225*(5227), 90–92, doi.org/10.1038/225090a0.

Mackay, D. M. (1970b). Interocular transfer of suppressive effects of retinal image displacement. *Nature*, *225*(5235), 872–873, doi.org/10.1038/225872a0.

Macknik, S. L., & Martinez-Conde, S. (2004). Dichoptic visual masking reveals that early binocular neurons exhibit weak interocular suppression: Implications for binocular vision and visual awareness. *Journal of Cognitive Neuroscience*, *16*(6), 1049–1059, doi.org/10.1162/0898929041502788.

Mante, V., Frazor, R. A., Bonin, V., Geisler, W. S., & Carandini, M. (2005). Independence of luminance and contrast in natural scenes and in the early visual system. *Nature Neuroscience*, *8*(12), 1690–1697, doi.org/10.1038/nn1556.

Matin, E., Clymer, A. B., & Matin, L. (1972). Metacontrast and saccadic suppression. *Science*, *178*(4057), 179–182.

Morgan, M. W. (1944). The clinical aspects of accommodation and convergence. *American Journal of Optometry & Archives of the American Academy of Optometry*, *21(8),* 301–313.

Saladin, J. J., & Sheedy, J.E. (1978). A population study of relationships between fixation disparity, heterophorias and vergences. *American Journal of Optometry and Physiological Optics*, *55(11),* 744–750.

Schiller, P. H., & Smith, M. C. (1968). Monoptic and dichoptic metacontrast. *Perception & Psychophysics*, *3*(3), 237–239, doi.org/10.3758/BF03212735.

Seriès, P., Lorenceau, J., & Frégnac, Y. (2003). The

"silent" surround of V1 receptive fields: Theory and experiments. *Journal of Physiology-Paris*, *97*(4–6), 453–474, doi.org/10.1016/j.jphysparis.2004.01.023.

Shapley, R. M., & Victor, J. D. (1981). How the contrast gain control modifies the frequency responses of cat retinal ganglion cells. *The Journal of Physiology*, *318*, 161–179.

Watanabe, J., Noritake, A., Maeda, T., Tachi, S., & Nishida, S. (2005). Perisaccadic perception of continuous flickers. *Vision Research*, *45*(4), 413–430, doi.org/10.1016/j.visres.2004.09.010.

Weisstein, N. (1971). W-shaped and U-shaped functions obtained for monoptic and dichoptic disk-disk masking. *Perception & Psychophysics*, *9*(3), 275–278, doi.org/10.3758/BF03212647.

Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Research*, *48*(20), 2070–2089, doi.org/10.1016/j.visres.2008.03.021.