

RESEARCH ARTICLE

Sensory Processing

Trans-retinal predictive signals of visual features are precise, saccade-specific and operate over a wide range of spatial frequencies

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Abstract

Saccadic eye movements successively project the saccade target on two retinal locations: a peripheral one before the saccade, and the fovea after the saccade. Typically, performance in discriminating stimulus features changes between these two projections is very poor. However, a short (~200 ms) blanking of the target upon saccade onset drastically improves performance, demonstrating that a precise signal of the peripheral projection is retained during the saccade. Although little is known about the nature of that transsaccadic signal, previous reports conjectured that it relies on information processed by the magnocellular system. Across two experiments, we investigated the feature blanking effect for a wide range of spatial frequencies (0.5–8 cycles per degree of visual angle, dva), stimulus sizes (1–4 dva), and eccentricities (6–10 dva). In each trial, participants executed a saccade to a high-contrast grating presented either left or right of fixation. During the saccade, the grating changed orientation (clockwise or counter-clockwise) either instantaneously or after a 200-ms blank, and participants reported the change's direction. We contrasted this saccade condition with a trans-retinal fixation condition mimicking the peripheral-then-foveal sequence of the target stimulus occurring across a saccade. Remarkably, blanking improved performance reliably for each spatial frequency, stimulus size, and eccentricity, but only in the saccade condition. Performance with blanking in saccade trials systematically exceeded performance in the fixation condition. Our results demonstrate a robust feature blanking effect across saccades, suggesting that transsaccadic processes involve low-level visual features beyond those processed in the magnocellular system.

NEW & NOTEWORTHY Across a saccadic eye movement, the visual system is able to keep track of the signals carrying the visual features of a saccade target. We provide evidence that these signals are sensitive to a wide range of stimulus sizes, can use a wide range spatial frequencies channels and, operate at various saccade amplitudes. Our results suggest an underlying mechanism operating beyond the magnocellular pathway that is contingent to saccade execution.

blanking effect; perception and action; spatial frequency; transsaccadic perception; visual pathways

INTRODUCTION

Primates actively explore their visual space by making saccadic eye movements (or saccades) to the locations of their interest in the visual field. Each of these >100,000 daily saccades has visual and computational consequences such as the relocation of objects on the retina, changes in visual resolution across the visual field, and the smearing of the input image during the movement (1, 2). Although these disturbances in the visual input have been treated as a nuisance, the visual system is remarkably efficient at dealing with them,

providing highly functional and phenomenologically stable and continuous vision. Nonetheless, the neural and cognitive mechanisms ensuring this continuity and stability are still poorly understood and are a matter of debate. One potential mechanism involves keeping track of the information available before the saccade to establish correspondence with information available once the saccade was made. Indeed, an object of interest that is the target of an imminent saccade initially projects onto the peripheral retina, creating a presaccadic image. Upon saccade landing, the same object falls on the foveal and parafoveal regions, creating the

postsaccadic image. Although initial attempts failed to show any significant influence of the presaccadic signal on postsaccadic processing or their integration (3–6), the past decade provided evidence that such integration does not only occur but is in fact also making nearly optimal use of imperfect visual signals. For example, presaccadic features such as color (7–10), motion (11, 12), and orientation (13–17) can be integrated with postsaccadic signals. Moreover, the integration of pre- and postsaccadic signals can have long-lasting effects, often referred to as transsaccadic re-calibration or learning (18, 19). In particular, some studies have demonstrated that repetitive transsaccadic changes to saccade target size, shape or its texture can bias the subsequent presaccadic percept itself (20–25). Moreover, a recent study demonstrated that training at discriminating transsaccadic orientation changes can lead to transsaccadic perceptual learning—a long-lasting improvement of visual sensitivity, rather than bias (26). Unlike classic perceptual learning, transsaccadic perceptual learning was shown to be unspecific to the trained location and therefore presents an important advantage for potential applications. Thus, understanding the nature of the transsaccadic mechanisms is of particular importance in view of novel and more efficient rehabilitation protocols in vision.

One effective way to study the content of presaccadic information right after a saccade is afforded by the blanking paradigm (27, 28). It consists in interrupting the presentation of a saccade target for a brief duration, typically ~200 ms from a detected saccade onset. Blanking grants access to the presaccadic information which otherwise is either masked, overwritten by, or integrated with the postsaccadic information. It drastically improves performance (typically by 20%–40%) at detecting and discriminating changes to the saccade target occurring during saccade. Capitalizing on this blanking paradigm, Deubel et al. (27) demonstrated that the presaccadic information relative to the location of a saccade target is not suppressed or lost as thought previously (29). Instead, it is very precise and accessible after a saccade if required by the observer's task. More recently, blanking has been shown to improve performance in discriminating transsaccadic changes of complex forms (30, 31) and visual features of the saccade target, including spatial frequency (32), orientation (33), and color (34).

Interestingly, a handful of studies have shown that the blanking effect is strongly reduced or even abolished under specific circumstances, informing us of a potential bottleneck of transsaccadic processing. In particular, blanking did not improve the discrimination of transsaccadic location displacements (35, 36) and transsaccadic changes of orientation (33) when the saccade target varied in color but had no luminance contrast to the background. These studies suggest that the presaccadic information carried across saccade is very poor when saccade targets are isoluminant. In addition, Balp et al. (37) found no blanking effect for transsaccadic orientation changes when using gratings of smaller size and higher spatial frequency as compared with stimuli used in studies that have found the feature blanking effect (33) or evidence for transsaccadic integration of orientation (13, 14, 17). Given the presumable bottleneck of presaccadic signal demonstrated by these studies, it is tempting to hypothesize that the transsaccadic information largely relies on the magnocellular system (36), which is sensitive to

luminance but not color contrast, has large receptive fields, and is tuned to low spatial frequencies (38, 39). Moreover, the neural transmission of the magnocellular pathway is fast which, given the short duration and high frequency of eye movements, might be a valuable characteristic for transsaccadic processing. In line with this idea, transsaccadic updating (40) and integration (41) can be fast, and electrophysiological correlates of presaccadic information emerge shortly after saccade landing (42, 43).

To this day, however, studies showing the influence of the presaccadic signals on the postsaccadic processing used a narrow range of stimulus dimensions, namely, spatial frequency and size, and strongly varied in methodology. For example, Fornaciai et al. (13) have used the delayed interference phenomenon to show transsaccadic integration where that task-irrelevant flanker gratings bias the orientation perception of a presaccadic grating. Wolf and Schütz (15) and Ganmor et al. (14) used plaid stimuli and standard Gabor gratings, respectively, to show that transsaccadic integration of orientation occurs in a close to optimal manner. In addition, although some of the studies have found transsaccadic effects being reproducible without saccades (12, 13), others have found these effects to be saccade-specific (14, 31). Hence, it remains unclear how much of the presaccadic information remains available after the saccade, nor what is its nature.

In the present study, we used the blanking paradigm to investigate the content of the transsaccadic signal in an orientation change discrimination task. We investigated a wide range of stimuli varying along the dimensions of size, eccentricity, and spatial frequency. Our aim was to 1) test whether the transsaccadic featural information is constrained to the features carried by the magnocellular pathway, i.e., luminance-defined stimuli that are large, of low spatial frequency, and in the visual periphery (44), 2) provide a solid basis for stimuli selection for future studies in the field of transsaccadic vision, and 3) assess the saccade contingency of the feature-blanking effect by comparing a saccade to a closely matched fixation task. To preface our results, we found a very robust feature blanking effect across all the dimensions tested. The results clearly indicate that the feature blanking effect occurs only in the context of a saccade but not during passive fixation.

EXPERIMENT 1

A number of studies have successfully demonstrated that presaccadic orientation signals can integrate with postsaccadic ones (13, 14, 16, 17). By adapting the original blanking paradigm to transsaccadic orientation change discrimination, Grzeczowski, Deubel et al. (33) have shown that the presaccadic target orientation can be accessed at the saccade offset, similarly to a target's location (27, 28, 30, 35, 37, 45), and that this signal is precise. Although it has been suggested that the presaccadic signal may rely mainly on the magnocellular pathway (35, 36), we currently lack empirical data showing which spatial frequency channels are able to carry those orientation signals across eye movements. *Experiment 1* tested the feature blanking effect across five different spatial frequencies comprising low [0.5–2 cycles per degree (cpd)], intermediate (4 cpd), and high spatial frequencies (8 cpd). If

the magnocellular theory were true, one should expect stronger blanking effect for low as compared with high spatial frequencies. These effects should be largest at higher stimulus eccentricities where the magnocellular pathway is dominant. Accordingly, the blanking effect in *experiment 1* was tested at 6 and 10 degrees of visual angle (dva) of eccentricity.

Methods

Participants.

Twenty naïve participants (mean age 26.20 ± 4.82 , range 20–36; 12 females) took part in the study. Our sample size was determined based on previous research (33) where the strength of the blanking effect for this particular task was found to be high ($d < 0.81$) or very high ($d < 1.81$) for much lower sample size ($n = 12$). Participants signed informed consent before the experiment and were compensated for their participation 8€/h. All procedures were in accordance with the Declaration of Helsinki and were approved by the local ethics committee (Department of Psychology, HU Berlin).

Setup and stimuli.

Participants sat in a quiet and dark room. Chin and forehead rests were used to minimize head movements. The viewing distance was 57 cm. The experiment was controlled by a PC running on Linux Ubuntu 18.04.5 LTS operating system. Gaze position of the dominant eye was recorded using a tower-mounted EyeLink 1000 (SR Research Ltd., ON, Canada) with

a sampling rate of 1,000 Hz. Stimuli were displayed on a ViewPixx, LCD monitor (VPixx Technologies) with a 1,920 pixel $\times$ 1,080 pixel resolution (52.5 $\times$ 29.5 cm) and 120 Hz refresh rate. Responses were recorded via a standard keyboard. Stimulus display, eye tracking, and response collection were controlled using Matlab (The MathWorks, Natick, MA) with Psychophysics (46, 47), EyeLink (48), and Palamedes (49) toolboxes. The fixation point was a “bull’s eye” composed of superimposed black (~ 0 cd/m²) and white (60 cd/m²) disks. The diameter of the fixation point was 0.8 degrees of visual angle (dva). Saccade targets were Gabor patches, 4 dva in diameter, composed of a black (~ 0 cd/m²) and white (60 cd/m²) sinusoidal grating and a spatial frequency of either 0.5, 1, 2, 4 or 8 cycles per degree (cpd; Fig. 1A). Stimuli were presented on a uniform, gray background (30 cd/m²).

Procedure.

Each trial started with a presentation of a fixation point in the screen center (Fig. 1, B and C) for a randomly chosen delay between 400 and 700 ms. Next, the first grating appeared either at 6° or 10° to the left or right side of fixation (randomly varied across trials). The grating’s orientation was randomly chosen from the following orientations: -73.5° , -64° , -54.5° , -45° , -35.5° , -26° , -16.5° , 16.5° , 26° , 35.5° , 45° , 54.5° , 64° , and 73.5° , with respect to vertical (0°), thus purposely avoiding cardinal directions, which are usually perceived more easily. Participants made a saccade toward the grating center upon stimulus detection. As soon as the eye

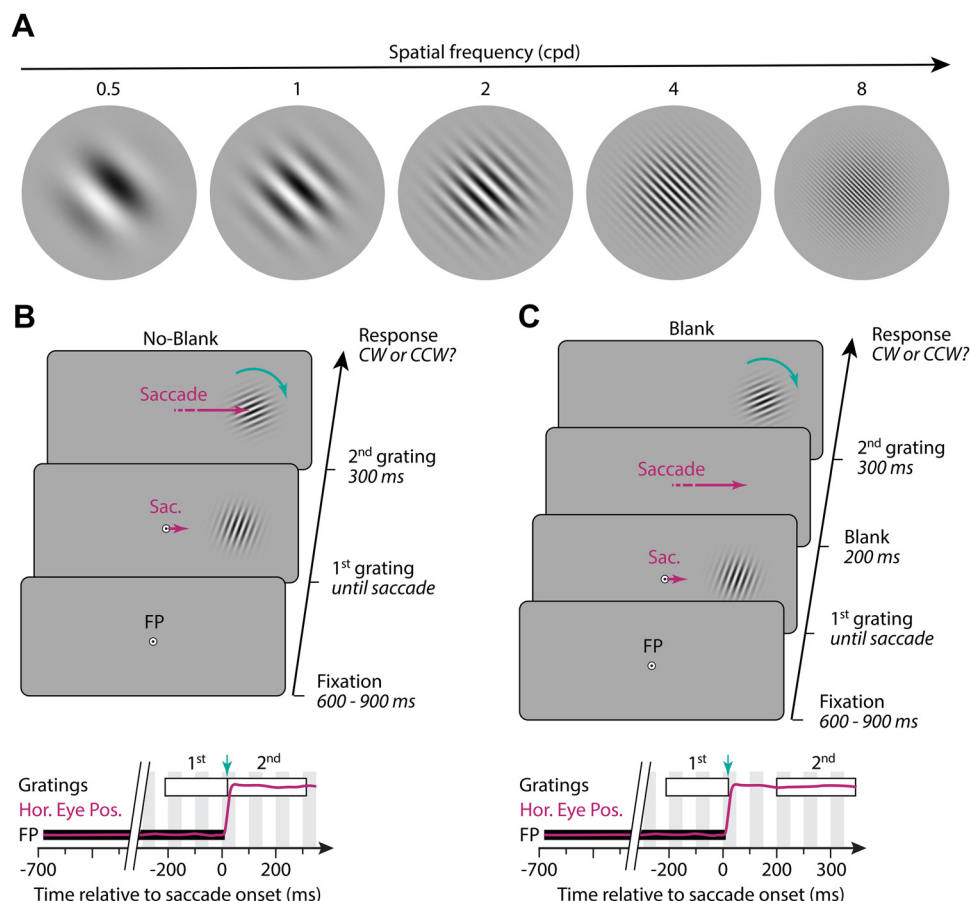


Figure 1. A: saccade targets used in *experiment 1*. B and C: Gabor gratings were presented randomly at 6 or 10 degree of visual angle (dva) from the screen center either on the left or right side from the fixation point (FP). Participants saccaded to the grating center and the saccade onset triggered the replacement of the first grating by the second one which differed in orientation. The second grating was presented either immediately (No-blank condition, B) or after a delay of 200 ms (Blank condition, C). After saccade landing, participants reported the orientation change direction of the second grating with respect to the first one (clockwise vs. counterclockwise).

position crossed the 2 dva-radius virtual border around the fixation point (saccade onset), the first grating was replaced by the second grating. That replacement was either immediate, occurring with the next screen refresh (No-blank condition, Fig. 1B), or delayed by 200 ms (Blank condition, Fig. 1C). The amplitude of the orientation change between the first and the second grating was chosen from a uniform prior distribution comprising angles between 0.1° and 25° in steps of 0.1° and controlled by an adaptive staircase procedure keeping correct responses at 75% (50). The second grating was presented for 300 ms. Participants judged the direction of the orientation change of the second grating with respect to the first grating as being clockwise or counterclockwise. Incorrect responses were followed by auditory feedback. After an intertrial interval of 500 ms, the next trial started. Previously, Grzeczowski, Deubel, et al. (33) demonstrated that this orientation change discrimination task is free of bias in both the Blank and the No-blank conditions, unlike the tasks in which the saccade target changes its location or color (51, 52). Hence, our dependent variable was the measured orientation change angle threshold between the two gratings (in degrees of arc). Trials in which participants made saccades before the first grating onset outside of the 2 dva radius fixation area, or earlier than 50 ms or later than 350 ms after the onset of the first grating were excluded from the staircase procedure and repeated at the end of the block. The same happened for trials in which saccades did not land inside a 2 dva radius area centered on the second grating or did not stay within that area for at least 50 ms after crossing its boundary or in which participants blinked during the trial. Participants performed 10 blocks of 160 trials each. Each block contained the same number of trials with the target being presented on both sides (left vs. right) and eccentricities (6° and 10°). Task difficulty for each eccentricity was continuously adapted by separate adaptive staircases composed of 80 trials each within the same block. No-blank and Blank conditions were tested in separate blocks and each block contained stimuli with a unique spatial frequency. Participants took breaks between the blocks whenever they felt such need and the experiment lasted ~ 1 h and 20 min.

Data preprocessing and saccade kinematics.

Preceding the behavioral analysis, the recorded eye-position data were processed offline for saccade detection, following the method proposed by Engbert and Mergenthaler (53). Saccade detection was based on the saccade velocity distribution using a moving average over 20 subsequent eye position samples. Onset and offset of saccades were detected when the velocity exceeded and fell behind the median of the moving average by 3 SDs for at least 20 ms. Because saccade kinematics are known to be influenced by factors such as spatial frequency or stimulus size of the saccade target, we report the saccade amplitude, duration, and latency based on these offline detected saccade onsets and offsets. Note however that video-based eye tracking is prone to some uncertainty caused by the postsaccadic oscillations (54, 55). Only trials in which a correct fixation was maintained within a 2.0 dva radius centered on the fixation point and a correct saccade as defined earlier by the online rejection criteria, starting from that fixation area and landing within a 2.0 dva radius area centered on the saccade target, were included. These rejection criteria resulted in the exclusion of 18.19% of trials in *experiment 1*, 15.69% and 5.67% of trials in *experiment 2* in the saccade and fixation task, respectively.

Results

A three-way repeated-measures ANOVA with factors blanking (No-blank and Blank), target eccentricity (6 and 8 dva), and spatial frequency (0.5, 1, 2, 4, and 8 cpd) was used for the statistical analysis. All three main effects were statistically significant. As evidenced by significantly lower thresholds, performance at detecting transsaccadic orientation changes was higher in the Blank condition across all the spatial frequencies tested for stimuli presented at both, 6 and 10 dva of eccentricity (Fig. 2, A and B; $F_{1,19} = 81.38$, $P < 0.001$, $\eta^2 = 0.171$). On average, blanking improved performance at detecting orientation changes by 23.27% (Fig. 2C). Performance was higher for stimuli presented at 6 dva ($F_{1,19} = 75.17$, $P < 0.001$, $\eta^2 = 0.080$). Moreover, performance gradually decreased with increasing spatial frequency ($F_{4,19} = 17.35$, $P < 0.001$, $\eta^2 = 0.202$). None of the aforementioned three

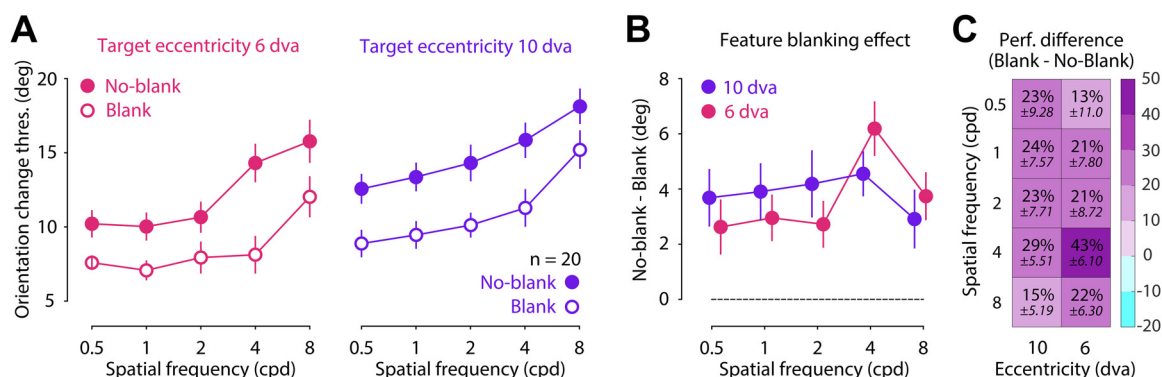


Figure 2. Results of *experiment 1*. A: performance as a function of spatial frequency and target eccentricity expressed as orientation change thresholds in the Blank vs. No-blank conditions. Performance was higher in the Blank condition across all the spatial frequencies and eccentricities. B: feature blanking effect as the orientation threshold difference between the No-blank and Blank conditions for saccade targets presented at 6 (red) and 10 dva (purple). The dashed line indicates the absence of the feature blanking effect. C: feature blanking effect as percentage of improvement from the No-blank to the Blank condition (i.e., Threshold No-Blank/Threshold Blank) for each saccade target eccentricity and spatial frequency. Means $\pm$ SE. cpd, cycles per degree.

factors interacted ($0.567 < F < 1.968$, $0.108 < P < 0.688$, $0.0001 < \eta^2 < 0.002$). Saccade amplitudes, durations, and latencies for targets at 6 and 10 dva were 5.86 ± 0.07 and 9.84 ± 0.08 dva, 34.63 ± 0.94 and 45.83 ± 1.18 ms, and 186.00 ± 4.25 and 180.91 ± 3.87 ms, respectively (means $\pm$ standard error of the mean) and did not differ as a function of spatial frequency.

EXPERIMENT 2

Experiment 1 successfully replicated the feature blanking effect (33) for a wide range of spatial frequencies from 0.5 to 8 cpd and at 6 and 10 dva of eccentricity. Interestingly, Balp et al. (37) reported a lack of this effect, when spatial frequency and eccentricity were within this range (4.5 cpd and 6–8 dva, respectively). But their stimuli strongly differed from ours in size (1 vs. 4 dva, respectively). In *experiment 2*, we tested nine combinations of size and spatial frequency including one highly similar to the one used by Balp et al. (37), namely a Gabor of 1 dva in diameter and a spatial frequency of 4 cpd. Moreover, although some of the studies found that transsaccadic mechanisms do not generalize to passive viewing conditions (14, 26, 31), others have found transsaccadic behavioral results to be comparable with those found at fixation (12, 13, 56). For example, using checkerboard-Phillips patterns (57), Grzeczowski, Van Leeuwen, et al., (31) found no evidence for blanking effect of object detail in a passive viewing condition but feature integration of a Vernier stimulus seems to be unaffected by a saccade (12). In *experiment 2*, we asked whether the feature blanking effect relies on saccade-specific mechanisms or if it generalizes to a condition in which participants maintain fixation while the stimulus undergoes a trans-retinal displacement mimicking the displacement across a saccade.

Methods

Setup, stimuli, and procedure.

The experiment was composed of two sessions, separated by at least 1 wk. The first session was identical to *experiment 1* except the following. Gaze position was recorded using a desktop-mounted EyeLink 1000 (SR Research Ltd., ON, Canada). The fixation was a dark (~ 0 cd/m²) dot of ~ 0.22 dva in diameter instead of the bull's eye. Gabor gratings had a spatial frequency of either 2, 4, or 8 cpd and a size (diameter) of 1, 2, or 4 dva (Fig. 3A) and were presented always at 8 dva eccentricity. In each block, the combination of one spatial frequency and one Gabor size was chosen randomly and remained constant throughout the block. Trials with and without a blank were randomly interleaved within each block. The amplitude of the orientation change was controlled by separate adaptive staircases for the No-blank and Blank conditions within the same block, consisting of 80 trials each. The second session took place at least 1 wk after the first session and followed the same procedure as the first session except that the task did not involve eye movements (Fig. 3B). In each trial, following the fixation period, the first grating was presented for 300 ms either on the left or right side from fixation (Fig. 3C). Unlike in the first session, participants did not saccade to the target and maintained their gaze at fixation point. Then the second grating was presented at the fixation location for 300 ms either immediately

(No-blank condition) or after a 200-ms delay (Blank condition). This presentation sequence aimed to mimic the pre- and postsaccadic retinal displacement occurring in the respective saccade task where participants were first presented with a peripheral Gabor followed by a Gabor in the foveal/parafoveal region. Twenty-three naïve participants (mean age 23.48 ± 3.54 , range 18–33, 13 females) took part in the study and received 10€/h for their participation. The experiment was composed of nine blocks per session, each of the sessions lasted approximately 1 h and 20 min.

Results

For each of the two tasks (saccade and fixation), a separate three-way ANOVA with factors blanking (No-blank and Blank), size (1, 2, and 4 dva), and spatial frequency (2, 4, and 8 cpd) was conducted. In the saccade task (Fig. 3D, left), orientation change thresholds were consistently lower in the blanking condition as compared with the No-blank condition ($F_{1,22} = 69.15$, $P < 0.001$, $\eta^2 = 0.235$). Moreover, orientation change thresholds moderately increased (i.e., performance decreased) as function of increasing spatial frequency ($F_{2,44} = 11.09$, $P < 0.001$, $\eta^2 = 0.059$). The size of the Gabor patch had no significant effect on task performance ($F_{2,44} = 0.32$, $P = 0.725$, $\eta^2 = 0.001$). None of the interactions between the three factors were significant ($0.148 < F < 2.140$, $0.130 < P < 0.863$, $0.0004 < \eta^2 < 0.010$).

In the fixation task (Fig. 3D, right), tested in the second session, blanking the target did not improve performance at all ($F_{1,22} = 0.154$, $P < 0.699$, $\eta^2 = 0.005$). Moreover, neither the size ($F_{2,44} = 0.169$, $P = 0.845$, $\eta^2 = 0.002$) nor the spatial frequency of the target ($F_{2,44} = 1.926$, $P = 0.158$, $\eta^2 = 0.014$) had an effect on task performance. None of the interactions between the three factors were significant ($0.103 < F < 1.308$, $0.281 < P < 0.981$, $0.0005 < \eta^2 < 0.006$).

Figure 3G shows the saccade metrics from the saccade task. Saccade amplitudes increased gradually with saccade target size ($F_{2,44} = 62.881$, $P < 0.001$, $\eta^2 = 0.425$). The duration of saccades made to saccade targets of 1 dva was significantly higher than those made to saccade targets of 4 dva ($F_{2,44} = 4.39$, $P = 0.018$, $\eta^2 = 0.041$). Saccade latencies were significantly higher for 8 cpd targets as compared with 2 and 4 cpd, irrespective of the target size ($F_{2,44} = 103.93$, $P < 0.001$, $\eta^2 = 0.670$). None of the remaining comparisons including saccade metrics (amplitude, duration, latency) differed as a function of spatial frequency or size.

DISCUSSION

Transsaccadic mechanisms keep track of the presaccadic signals until after a saccade may play a crucial role in establishing visual continuity across eye movements at the functional and phenomenological levels. Previously, little was known about how much of the presaccadic signal is retained throughout the saccade, nor its spatio-temporal characteristics. Here, we adapted a feature-blanking paradigm (32, 33) that enabled us to study transsaccadic orientation discrimination for a wide range of stimulus conditions. Saccade targets were high-contrast gratings of various combinations of spatial frequency and size and were presented at different eccentricities. Because our task required a comparison between orientations of a peripheral, presaccadic grating

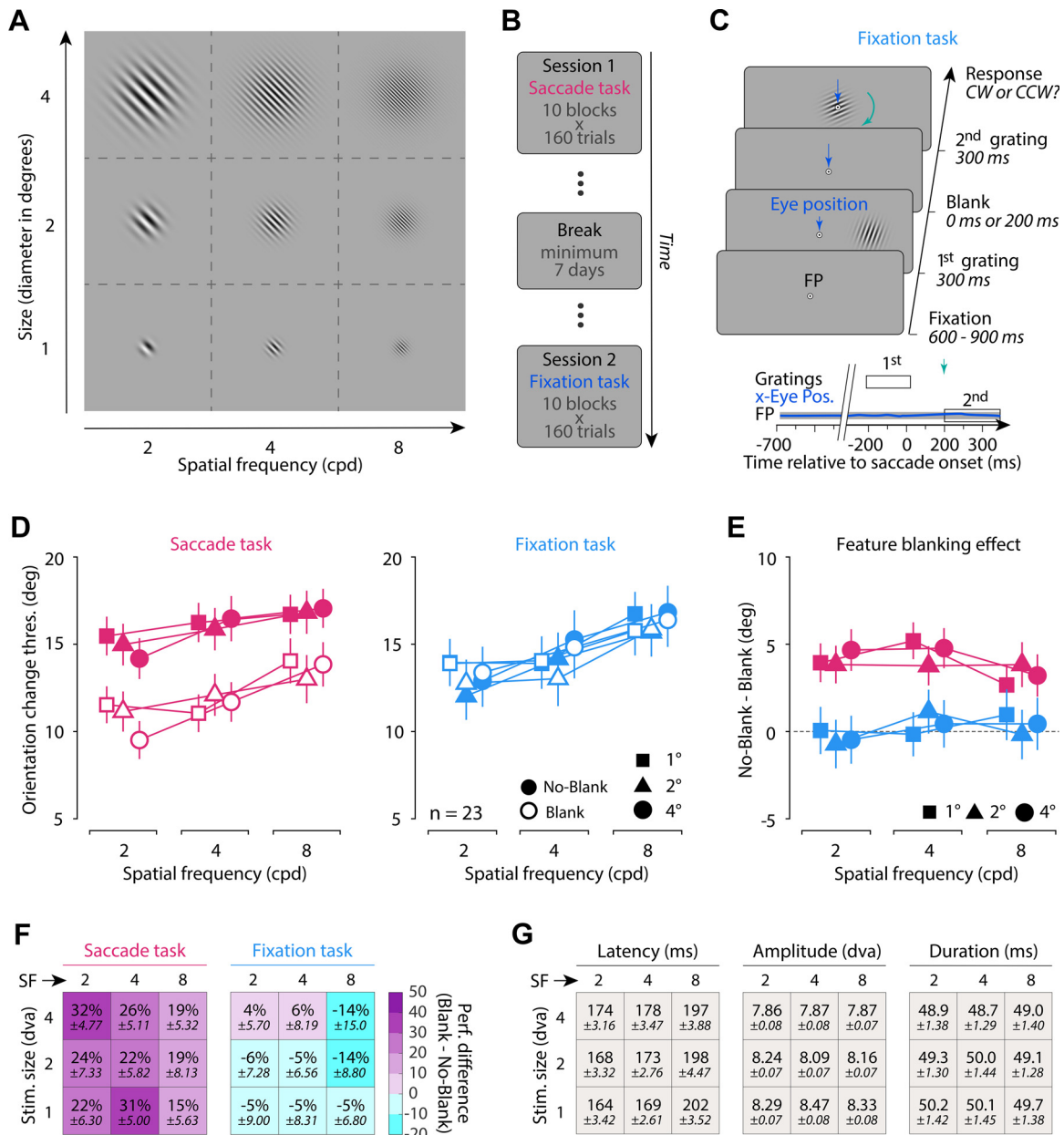


Figure 3. *A*: range of sizes and spatial frequencies of the saccade target. *B*: the experiment consisted of two sessions separated by a minimum of 1 wk. During the first session, the task was almost identical to *experiment 1*, where participants discriminated the orientation changes of gratings occurring during eye movements. In the second session, the task was the same, except that participants kept fixating in the screen center throughout the trial while being presented with a peripheral grating at first, followed by a second grating presented either immediately (No-blank condition) or after a 200-ms delay (Blank condition). The second grating was presented in the screen center, thus mimicking the retinal displacement of the stimulus in a saccade trial, *C* and *D*: orientation change thresholds as a function of spatial frequency and target size in the Blank vs. No-blank conditions for the saccade (red) and fixation (blue) task. In the saccade but not fixation task, blanking strongly improved performance. *E*: feature blanking effect as the difference between the No-blank and Blank conditions for the saccade (red) and fixation (blue) conditions. The dashed line indicates the absence of the feature blanking effect. *F*: feature blanking effect across saccade target sizes and spatial frequencies represented as percentage of improvement from No-blank to Blank condition for the saccade and fixation task. *G*: average saccade latencies, amplitudes, and durations across different spatial frequencies and sizes of the saccade target in the saccade task. Means $\pm$ SE. cpd, cycles per degree; dva, degree of visual angle.

with a foveal, clearly visible postsaccadic grating, an improvement of performance in the task demonstrates an increased access to the content of the presaccadic signal. Across two experiments, we found very consistent and robust evidence showing that blanking the saccade target strongly improves performance as compared with the No-blank condition ($\eta^2 = 0.171$ and 0.235 , for *experiment 1* and *experiment 2*,

respectively) for all tested spatial frequencies (0.5, 1, 2, 4, and 8 cpd), sizes (1, 2, and 4 dva), and eccentricities (6, 8 and 10 dva) of the saccade target.

In *experiment 1*, we found that performance was better for stimuli presented closer to the fixation (6 dva) than for stimuli placed further away (10 dva) that likely reflects the retinal inhomogeneity of photoreceptor distribution (58). In addition,

we found the blanking effect to be larger for high spatial frequencies at 6 dva but at 10 dva it was larger for low and medium spatial frequencies (*experiment 1*; Fig. 2B). This difference was pronounced for some, but not all participants and a similar condition in *experiment 2* (Fig. 3E, red disk) did not show such increase of performance from 2 cpd to 4 cpd. Hence, it is unclear whether the difference in *experiment 1* represents a real effect or simply a fluke. We found that performance decreased as a function of increasing spatial frequency in both experiments. This relation was strong in *experiment 1* only, probably due to a wider range of spatial frequencies, and moderate in *experiment 2* for the saccade task. It was not significant in the fixation task.

Previous studies suggested that the presaccadic signals carried across a saccade might mainly rely on the magnocellular pathway because luminance contrast plays a key role in transsaccadic processing (15, 33, 35, 36). Our results clearly show that the range of the presaccadic signal that can be retained across an eye movement goes beyond the magnocellular pathway characteristics as it is not limited to low-spatial frequencies (e.g., 0.5–2 cpd) or large stimuli (e.g., 4 dva).

It seems that as soon as the saccade target can be detected in the periphery, a precise orientation signal of the presaccadic stimulus can be retained across a saccade independently of the stimulus spatial frequency, size, or eccentricity. Previously, similar results have been found when luminance contrast of oriented gratings was manipulated (33). Unlike the location blanking effect (35), the orientation blanking effect did not ramp up gradually with increasing luminance contrast but rather reached the full improvement due to blanking (24%) with the lowest (but visible) luminance contrast. Here, we found similar results for size, spatial frequency, and eccentricity (Fig. 3E).

Finally and surprisingly, we found no evidence that the size of saccade target matters at all. One aim of our study was to test a wide range of stimuli including those from recent incongruent findings that have (33) and have not (37) found the feature blanking effect and therefore to understand the characteristics of the transsaccadic processing bottleneck. Balp et al. (37) have used high-contrast, 1 dva gratings with a spatial frequency of 4.5 cpd. They have found that blanking the saccade target improves the location but not the orientation change discrimination. In *experiment 2*, we used similar stimuli (1 dva, 4.0 cpd) and found strong improvements in performance due to blanking (+31%) in that condition. Although we can only speculate about the differences between Balp et al. (37) and our study, one difference might be particularly significant. In our study, before the presentation of the saccade target in periphery, participants fixated a task-irrelevant fixation stimulus, while Balp et al. (37) presented the target itself already during that fixation period (called “F”; their Fig. 1). Therefore, participants did not have to extract the orientation signal from the peripheral presentation of the stimulus (called “T”) because it was already provided at fixation (“F”). Hence, the task could have been solved by comparing a presaccadic foveal signal (“F”) with the postsaccadic, foveal signal (“TD”) which is different from our design and from the retinal displacement of stimuli across saccades in natural vision. The relatively long exposure to the oriented stimulus throughout the fixation

(~250–500 ms) and the foreperiod (duration not provided by the authors) but also after saccade offset (600 ms) in the same retinal location (foveal) might also have adapted participants to the stimulus’ orientation, potentially interfering with the task. Moreover, by giving the possibility of perceiving the presaccadic stimulus foveally “long” before the saccade at fixation, the task may have tapped very different mechanisms than in our study. In agreement with this interpretation, in the location discrimination task for which a strong blanking effect was found in the same study, the location of the target had to be extracted from the peripheral presaccadic signal (“T”) as it was not provided at fixation (“F”).

In *experiment 2*, we tested whether the feature blanking effect also occurs in a task where participants do not make eye movements but instead are passively exposed to a peripheral-then-foveal stimulus, thus mimicking the visual displacement occurring across a saccade. No blanking effect was found in this fixation task for any combination of size and spatial frequency. Importantly, these results suggest that the mechanism used in retaining the presaccadic signal is saccade-specific and that it is precise in nature. In agreement with this idea, blanking detailed images or Phillips patterns (57) improves performance at discriminating image changes that occurred during saccades (30, 31) but does not influence performance in different fixation tasks (31). Note however that the fixation task was not perfectly mimicking the retinal stimulation that occurred during the saccade task. For example, the duration of peripheral Gabors differed in both tasks as in the fixation task the duration was fixed (300 ms) whereas in the saccade task it depended on the saccade latency. Nevertheless, even close-to-perfect mimicry of the retinal stimulation that occurs during saccade in a fixation condition appears to have no effect on trans-retinal integration (59).

Thus, our results significantly add to the evidence suggesting that the same or similar visual tasks performed in relation to action (e.g., eye movements) may rely on different or additional mechanisms as those performed during passive vision tasks. Some evidence suggests that learned visual tasks within an active framework may reflect distinct or additional mechanisms than within the passive vision framework. For example, it has been demonstrated that visual tasks involving an adjustment method do not transfer to binary forced choice variants of the same (or similar) task and vice versa suggesting different encoding mechanisms (60–62). Moreover, visual perceptual learning with eye movements has important advantages over classic visual learning protocols (26, 63). For example, we have recently shown that one of the hallmarks of visual perceptual learning—location specificity—can be overcome by training using transsaccadic predictive mechanisms (26) which may be a crucial finding for rehabilitation protocols, sports, or education.

Our results are compatible with several previously proposed predictive, transsaccadic mechanisms (31, 33, 64, 65) that could play a role in establishing visual stability through remapping of the visual features, or even generating a preattentive visual analog (66). It has been proposed that presaccadic stimulus features are retained across a saccade through a predictive mechanism, in which the presaccadic signal reaches higher visual areas feedforward before it is fed back to lower-visual areas at the predicted spatiotopic

location (33, 64, 65), or for the saccade target (as in our case), simply the fovea (67). The neural activations of low-level neurons by high-level neurons would give rise to phantom-like percepts (15), similar to filling-in phenomena (68). These could serve as an anchor that helps establish the correspondence between pre- and postsaccadic projections of the world onto a retinotopic reference frame, supporting visual stability.

Whereas in *experiment 1* we did not find any differences related to the oculomotor behavior in different conditions, in *experiment 2*, saccade amplitudes were larger and durations were longer for bigger stimuli and, latencies were slower for higher spatial frequencies (Fig. 3G). Both of these effects have been shown previously. The saccade's specific landing point is determined by pooling of information gathered from the shape of the target object (69) and saccade latencies were shown to decrease as a function of contrast, and increase with spatial frequency (70). In *experiment 1*, stimuli were presented at two different eccentricities that likely prevented the impact of target size on amplitude; this was not the case in *experiment 2*. The influence of the saccade target's spatial frequency on latency was shown to occur between low and intermediate versus high spatial frequencies, i.e., above 7 cpd (70) which explains the lack of an effect in *experiment 1* in which 4 out of 5 spatial frequencies were below 7 cpd.

We studied the content of the presaccadic signal in a transsaccadic orientation change discrimination task with a wide range of oriented gratings using an adapted version of the blanking paradigm. We found that the presaccadic orientation signal that is retained across a saccade is precisely encoded and is not confined to specific spatial frequency channels, receptive field sizes, or target eccentricities. Moreover, our results demonstrate that the retention of the signal from peripheral to foveal location occurs only when a saccade is executed but not during passive fixation, emphasizing the importance of studying the visual processes in tight relation to action.

DATA AVAILABILITY

Data will be made available upon reasonable request.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

L.G., A.S., and M.R. conceived and designed research; L.G. and A.S. performed experiments; L.G. analyzed data; L.G. and M.R. interpreted results of experiments; L.G. and A.S. prepared figures;

L.G. drafted manuscript; L.G. and M.R. edited and revised manuscript; L.G., A.S., and M.R. approved final version of manuscript.

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