Remapping versus short-term memory in visual stability across saccades

Rodrigo Balp¹ · Florian Waszak¹ · Thérèse Collins¹

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Abstract

Saccadic eye movements cause displacements of the image of the visual world projected on the retina. Despite the ubiquitous nature of saccades, subjective experience of the world is continuous and stable. In five experiments, we addressed the mechanisms that may support visual stability: matching of pre- and postsaccadic locations of the target by an internal copy of the saccade, or retention of the visual attributes of the target in short-term memory across the saccade. Healthy human adults were instructed to make a saccade to a peripheral Gabor patch. While the saccade was in midflight, the patch could change location, orientation, or both. The change occurred either immediately or following a 250-ms blank during which no visual stimuli were available. In separate experiments, subjects had to report either whether the patch stepped to the left or right or whether the orientation rotated clockwise or counterclockwise. Consistent with previous findings, we found that transsaccadic displacement discrimination was enhanced by the addition of the blank. However, contrary to previous findings reported in the literature, the feature change did not improve performance. Transsaccadic orientation change discrimination did not depend on either an irrelevant temporal blank or a simultaneous irrelevant target displacement. Taken together, these findings suggest that orientation is not a relevant visual feature for transsaccadic correspondence.

Keywords Eye movements · Cognitive processing

The visual world appears stable and continuous, even though the actual input to our visual brain is constantly changing: interrupted by blinks, smeared by eye and head movements, and shifted by saccades. Saccades are fast movements of the eye that reposition the high-acuity part of the retina, the fovea, on objects of interest, at a rate of approximately 3–4 Hz. One of the classic questions about visual perception is how stable visual percepts arise in the face of this highly variable and discontinuous input.

In this article, we are interested in the mechanisms that support transsaccadic correspondence—in other words, the mechanisms that match the various retinal locations of a given visual object across a saccade, giving rise to a unified and stable percept. There have been several theoretical proposals as to how this matching process occurs.

According to the remapping point of view, a motor signal is combined with the retinal consequences of the saccade so as to

establish a correspondence between two locations. The initial proposal was that the motor signal “canceled out” the self-caused retinal signal, as if the motor signal were a kind of negative image of the retinal input. Although such a negative-image-like signal has been shown to prevent self-stimulation in electric fish (Bell, 1981), in primates this is unlikely (Sommer & Wurtz, 2004). Rather, a copy of the saccade command (called the *effERENCE COPY* or *COROLLARY DISCHARGE*) allows the activity evoked by a stimulus at a particular retinal location to be transferred to neurons whose classic receptive field (RF) is not at that location, but in whose RF the stimulus will fall after the saccade. In this way, remapping allows the past and present retinal locations of a visual object to be aligned; when remapping is predictive, it allows the current and future retinal locations of an object to be matched. Remapping has been shown to occur in neurons (Duhamel, Colby, & Goldberg, 1992; Sommer & Wurtz, 2006; Umeno & Goldberg, 1997; Walker, Fitzgibbon, & Goldberg, 1995) and in behavior (Rolf, Jonikaitis, Deubel, & Cavanagh, 2011). In physiological terms, remapping could occur because each neuron is potentially activated by a stimulus at all possible retinal locations; the connections that transfer activity would vary according to planned movements. Remapping could also result from lateral

✉ Thérèse Collins
therese.collins@parisdescartes.fr

¹ Laboratoire Psychologie de la Perception, Université Paris Descartes & CNRS, 45 rue des Saint-Pères, Paris, France

connections that transfer activity from one retinal location to the other within a given brain area. This lateral transfer of activity is more physiologically plausible than massive feed-forward connections (Casagrande & Kaas, 1994).

A modern instantiation of the remapping account of visual stability is the *attention pointer account* (Cavanagh, Hunt, Afraz, & Rolfs, 2010). A corollary discharge (CD) signal allows activity in a saccade map (such as lateral intraparietal area, frontal eye fields, or superior colliculus) to be transferred from neurons whose RF corresponds to the presaccadic retinotopic location of the object to neurons whose RF corresponds to its postsaccadic location, and that activity feeds back to visual brain areas (V1–V4, MT), thus associating two retinotopically distinct locations into a single object representation and allowing features at the postsaccadic locations to be enhanced. Only attended objects are thought to be remapped (Joiner, Cavanaugh, & Wurtz, 2011), which limits the computational load. The attention pointer account is similar to several other proposals of how a descending saccade signal determines transsaccadic correspondence and the content of attention (visual attention model: Schneider, 1995; reentry hypothesis: Hamker, 2003). According to these proposals, the descending activity is blind with regard to features; it selectively activates neurons with a particular retinotopic RF, independently of their feature selectivity. According to the remapping account of visual stability, establishing object correspondence across a saccade depends on the spatial match between the actual postsaccadic target and its predicted location, which in turn depends on the CD.

However, remapping cannot be the only mechanism behind visual stability, because CD signals are notoriously imperfect in space and time (Grueser, Krizic, & Weiss, 1987; Honda, 1989, 1991; Matin, 1986). Even small discrepancies between the corollary discharge and the actual saccade should break visual stability, but this virtually never happens.

An alternative account of visual stability is that it relies on visual information about the pre- and postsaccadic scenes (Hollingworth, Richard, & Luck, 2008). In this case visual short-term memory (VSTM) is the crucial mechanism. A rich body of literature has shown that the quality of information retained across a saccade is coarse and abstract (Henderson, 1994; O'Regan, 1992; Pollatsek, Rayner, & Collins, 1984), which limits the computational load. According to the object-file theory of transsaccadic correspondence, about four object “files” can be retained across a saccade. Each object file integrates information such as color, position, or identity, such that adding the requirement to recall a supplementary visual attribute of one of the objects does not degrade performance (Irwin & Andrews, 1996). The saccade target itself benefits from prioritized encoding into VSTM (Irwin & Gordon, 1998), and a variant of the object-file theory proposes that a search process attempts to locate the target object after every saccade, based on remembered visual features of the

presaccadic object (Deubel, Schneider, & Bridgeman, 2002; McConkie & Currie, 1996). However, attempts to measure such a search have not been successful (Eymond, Cavanagh, & Collins, 2016; Jonikaitis & Theeuwes, 2013). According to the VSTM account of visual stability, establishing object correspondence across a saccade depends on similarity between the visual features before and after the saccade.

These two accounts of visual stability make different hypotheses as to the causal or consequential role of features in visual stability: according to the attention pointer account, features are matched across a saccade as a consequence of a transsaccadic correspondence between locations. According to the VSTM account, a transsaccadic correspondence between features causes locations to be matched.

In all likelihood, visual stability depends on some combination of remapping and VSTM. Indeed, the saccade target is prioritized, but objects close to the saccade target are recalled better than objects farther away, which means that location information plays a role (Irwin & Gordon, 1998). In a free-viewing situation in which the target is not specified in advance, attention benefits correlate with the actual landing position of the saccade (Doré-Mazars, Pouget, & Beauvillain, 2004), suggesting that transsaccadic correspondence relies on the specific metrics of the saccade, not only on the visual target location (which can differ because of oculomotor noise; see also Collins, Rolfs, Deubel, & Cavanagh, 2009).

In the laboratory, visual stability is often probed with the in-flight displacement task, in which participants make a saccade to a peripheral target. During the saccade, the target is displaced, and participants detect the displacement or discriminate its direction. Participants are notoriously bad at this task (Bridgeman, Hendry, & Stark, 1975), a phenomenon called *saccadic suppression of displacement* (SSD). SSD can be relieved by adding a brief irrelevant blank (i.e., with no visual stimuli) between the end of the saccade and the reappearance of the target in the displaced location (Deubel, Bridgeman, & Schneider, 1998; Deubel, Schneider, & Bridgeman, 1996), or an irrelevant displacement orthogonal to the saccade (Wexler & Collins, 2014). Thus, when there is a discrepancy between the postsaccadic location of the target and its remapped location, visual stability suffers. Furthermore, the specific metrics of the saccade are known to the visual system, because oculomotor noise is not confounded with object displacement (Collins, 2014; Collins et al., 2009). These results argue in favor of the importance of spatiotemporal information in establishing transsaccadic correspondence, in line with the remapping account.

However, SSD is also relieved when some visual features of the object change simultaneously with the displacement. When a change in location is accompanied by a change in shape (Demeyer, De Graef, Wagemans, & Verfaillie, 2010), polarity, or identity (Tas, Moore, & Hollingworth, 2012), the displacements are unmasked. In other words, transsaccadic correspondence is enhanced when the pre- and postsaccadic

objects share features, which argues in favor of transsaccadic feature correspondence as gating location correspondence, in line with the VSTM account.

The in-flight displacement task is thus an important paradigm for understanding the interplay between remapping and VSTM in visual stability. In the present study, we combined the in-flight displacement task with a feature change. In five experiments, participants had to make a saccade to a peripheral Gabor patch. During saccade execution, the patch could be displaced, its orientation changed, or both. In the first experiment (1a), we replicated saccadic suppression of displacement with the Gabor stimulus (no orientation shifts occurred). In the second and third experiments (1b and 1c), participants reported in which direction the patch had stepped, ignoring any orientation shifts. In the fourth and fifth experiments (2a and 2b), participants reported in what direction the orientation had shifted, and the patch displacements were task-irrelevant. In all experiments, we compared blank with no-blank conditions.

If matching features in VSTM drives visual stability, then breaking visual stability with an orientation shift should unmask transsaccadic displacements; we should observe an inverse relationship between the thresholds for displacement discrimination and orientation shift size (Exps. 1b and 1c). We compared the improvement with orientation shift to the improvement due to blanking, but had no specific hypotheses about any difference in magnitude between the two.

If a spatiotemporal remapping signal drives visual stability, then breaking visual stability with a displacement should unmask transsaccadic changes in orientation (Exps. 2a and 2b). Tas, Moore, and Hollingworth (2014) showed that when object continuity was broken by a blank, subjects were better able to correctly report the color of the presaccadic object. Without a blank, they tended to report the color of the postsaccadic target, as if the postsaccadic features had overwritten the presaccadic features. This idea is akin to masking: Postsaccadic features may mask presaccadic features, but this depends on the temporal proximity between the two sets of features. In our setup, breaking object continuity with a displacement should allow pre- and postsaccadic features to be accessed and compared better; we should observe an inverse relationship between the thresholds for orientation shift discrimination and displacement size. Again, we had no specific hypotheses about a difference in the magnitudes of improvement due to blanking or displacement.

Experiment 1a: Displacement (report displacement)

Method

Subjects Nine healthy human adults (six men, three women, 33 ± 12 years old) participated. All reported normal or

corrected-to-normal vision and no oculomotor or neurological impairments, received payment of €10/h for their time, and provided informed consent.

Stimuli and procedure The fixation stimulus was a Gabor patch with a diameter of 1 deg of visual angle (dva) and a spatial frequency of 4.5 cycles per degree (cpd). The contrast was 100%, and the patch was presented on a light gray background (30 cd/m^2). Figure 1 illustrates the experiment's geometry. Initially, the Gabor patch was randomly presented at position F inside an imaginary 2.45-dva-sided square at screen center. Its orientation was always vertical. Once the eyetracker had detected fixation, the Gabor patch remained visible for 250–500 ms, after which it disappeared, to immediately reappear at position T either 6 or 8 dva to the left or right. Subjects were instructed to follow the target by making a saccade from F to T . At saccade onset, the target disappeared and reappeared in position TD , which was T displaced by one of eight possible magnitudes (± 2.0 , ± 1 , ± 0.5 , or ± 0.25 dva). Reappearance of the Gabor patch occurred either immediately (*no-blank condition*) or after a 250-ms delay, during which no stimuli were present on the screen (*blank condition*). The stimulus remained in its final position TD for 600 ms. Subjects were instructed to respond whether the displacement from position T to position TD had been to the left or to the right, tapping the corresponding arrow key on the keyboard.

The experiment was carried out in a randomized factorial design, with two saccade directions (left/right), two saccade amplitudes (6/8 dva), eight target displacements (± 2.0 , ± 1 , ± 0.5 , ± 0.25 dva), two onsets (no blank, blank), eight repetitions in four blocks, yielding 520 trials per participant, divided into four blocks of 128 trials. Prior to the first block, participants performed a 20-trial practice, to get accustomed to performing the saccade and perceptual tasks.

We hypothesized that displacement discrimination performance would be better in the blank than in the no-blank condition, replicating previous work (e.g., Deubel et al., 1996). We also examined the point of subjective equality (PSE), which corresponds to the stimulus level at 50%. We hypothesized that the PSE would depend on blanking, with PSEs being closer to zero in the blank than in the no-blank task, although this effect has been less robustly reported in the literature (Deubel et al., 1996; Wexler & Collins, 2014). Note that a negative PSE corresponds to a forward bias (see the Discussion section).

Apparatus Stimuli were presented on a Sony GDM-F520 CRT monitor with $1,024 \times 768$ (width by height) pixel resolution at a 170-Hz refresh rate inside a 50.3×37.7 cm area. Responses were given by subjects via a standard keyboard. Saccadic eye movements were recorded using an EyeLink 1000 (SR Research Ltd., Mississauga, Ontario, Canada) operated in monocular mode at 1000 Hz, tracking the right eye,

Fig. 1 Example of a trial with a leftward saccade. Initially, the fixation Gabor is displayed within a centered dashed square at position F (the square is displayed for illustration purposes, and the white dot represents the center of the screen). The fixation stimulus was replaced by a target stimulus either 6 or 8 dva to the left at position T. When a

saccade toward the target was detected, the target disappeared and was replaced, either immediately (no-blank condition) or 250 ms later (blank condition), by a stimulus at position TD (one of the eight final locations, shown as small squares). The subject's task was to report the horizontal direction of the final target step, responding either "left" or "right"

with the EyeLink toolbox extension for Matlab (Cornelissen, Peters, & Palmer, 2002). Participants used forehead and chin rests and sat 57 cm away from the screen. Stimuli were generated using the Psychophysics Toolbox extensions for Matlab (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007).

Eye movement acquisition Viewing was binocular, and movements of the right eye were monitored with an EyeLink 1000 (SR Research, Mississauga, Ontario, Canada) at a 1000-Hz sampling rate. At the beginning of each experiment and each block, the eyetracker was calibrated using the standard nine-point EyeLink procedure.

Saccades were detected online when the horizontal component of gaze differed by more than 20% of the F – T distance. The eye movement traces were stored for offline analysis. For the offline analyses, the eye movement samples were smoothed with SR Research's proprietary algorithms. Instantaneous velocity and acceleration were computed for each data sample and compared to a threshold ($30^\circ/\text{s}$ and $8000^\circ/\text{s}^2$). Saccade onset was defined as two consecutive above-threshold samples for both criteria. Saccade offset was defined as the first sample of a 20-ms period of below-threshold samples.

We checked that gaze-contingent changes occurred during the saccade. On average, saccade duration was 43 ± 3 ms, which left ample time for the saccade to be detected and the gaze-contingent change to occur within the 6 ms granted by a 170-Hz refresh rate. We eliminated trials in which the eye movement occurred too early (% eliminations given in the Data Analyses section of each experiment) or too late ($< 1\%$ for all experiments).

Data analyses All data analyses were performed in Matlab (The MathWorks, Natick, 2014) and R (R Core Team, 2016). Perceptual performance was analyzed by fitting individual cumulative Gaussian functions to the proportion of "forward" responses (maximum likelihood method). The difference in

displacement size between the .5 and .75 points on the psychometric curve represented the perceptual threshold. We also examined the PSE. All fits were performed on the individual data. The reported means are based on these individual fits.

To assess the statistical significance of our effects, we used confidence intervals obtained by bootstrapping. We also assessed the evidence in favor of the null versus alternative hypotheses using Bayesian t tests (Rouder, Speckman, Sun, Morey, & Iverson, 2009) with the BayesFactor R package (Morey & Rouder, 2015; R Core Team, 2016).

We eliminated trials on the basis of eye movement behavior, so as to keep trials in which subjects performed the saccade task correctly. Subjects sometimes initiated the eye movement before the appearance of the target, and we did not include those trials in the analysis (12%). We also eliminated all trials in which saccade amplitude or latency was more than two standard deviations away from the average ($< 1\%$).

Results

The basic saccade characteristics were normal for visually guided saccades and did not differ between the blank and no-blank conditions. The average latencies were 180 ms (95% bootstrapped confidence interval: [162–201 ms]) in the blank condition and 177 [162–190] in the no-blank condition. The saccade amplitudes were 6.8 [5.9–7.7] and 6.8 [5.8–7.7] in the blank and no-blank conditions.

Figure 2a shows individual psychometric functions, and Figs. 2b and 2c show individual and average thresholds and PSEs in the blank and no-blank conditions. On average, performance was better in the blank condition (threshold of 0.53 dva, 95% confidence interval [0.41–0.65]) than in the no-blank condition (1.10 [0.73 to 1.48] dva). A Bayes factor analysis comparing the hypothesis that performance was better in blank than in no-blank conditions to the null hypothesis of equal thresholds between blank and no-blank conditions revealed evidence in favor of the alternative hypothesis ($\text{BF} = 4.96$).

Fig. 2 (a) Individual psychometric functions in the blank (gray) and no-blank (black) conditions. (b, c) Average (circles) thresholds (b) and PSEs (c), with 95% confidence intervals (triangles). Individual subjects are represented by dashed lines

The PSE also depended on blanking, with negative PSEs in the no-blank condition (-1.23 [-1.7 to -0.74]) and PSEs close to zero in the blank condition (0.08 [-0.23 to 0.38]). The Bayes factor was 5,339—evidence in favor of the alternative hypothesis of more negative PSEs in the no-blank than in the blank condition, over the null hypothesis of no difference in PSEs between the blank and no-blank conditions.

In sum, Experiment 1a established that we were able to replicate the classic blanking effect in our setup. We now moved on to Experiment 1b, in which in addition to the intrasaccadic target step, we added an irrelevant orientation shift.

Experiments 1b and 1c: Displacement and orientation shift (report displacement)

Method

Subjects Seven healthy human adults (four men, three women; 35 ± 16 years old) participated in Experiment 1b, and seven in Experiment 1c (five women, two men; 27 ± 6 years old). All reported normal or corrected-to-normal vision and no oculomotor or neurological impairments, received payment of €10/h for their time, and provided informed consent.

Stimuli and procedure Experiment 1b was identical to Experiment 1a, except the orientation of the Gabor patch at position F was not always vertical, but was randomly selected from the range 45 – 135 deg. The patch kept its orientation during the F to T displacement and underwent the orientation shift

simultaneously with the horizontal displacement (T to TD). Subjects were instructed to report the direction of the displacement (left/right) and to ignore any changes in orientation.

Experiment 1b was carried out in a randomized factorial design, with two saccade directions (left/right), two saccade amplitudes ($6/8$ dva), eight target displacements (± 2.0 , ± 1 , ± 0.5 , ± 0.25 dva), two onsets (no blank, blank), six orientation shifts (± 18 , ± 9 , ± 3 deg), and five repetitions, leading to a total of 1,920 trials, divided into 12 blocks. Experiment 1c was identical, except that there were only four orientation shifts (± 45 , ± 3 deg), leading to a total of 1,280 trials, divided into seven blocks.

We hypothesized that performance would be better in blank than in no-blank conditions, and that performance would also improve with the addition of the orientation shift. We hypothesized that the PSEs would be closer to zero in the blank condition, and more so with greater orientation shifts.

The apparatus and eye movement acquisition were identical to those aspects of Experiment 1a.

Data analyses Performance was analyzed as before (threshold, PSE). We tested our hypotheses by performing linear mixed-effect analyses on both measures using the lme4 R package (Bates, Maechler, Bolker, & Walker, 2015). As fixed effects, we included blank (blank, no blank) and orientation shift (± 18 , ± 9 , ± 3 deg in Exp. 1a, and ± 45 , ± 3 deg in Exp. 1b). The random structure comprised a random intercept by subjects. Significant effects were defined as those having a t value ≥ 2 .

We eliminated trials on the basis of the same criteria as previously: Trials in which the eye movement was initiated before the appearance of the target (Exp. 1b: 9%; Exp. 1c: 10%) and in which the saccade amplitude or latency was more than two standard deviations away from the average ($< 1\%$).

Results

In Experiment 1b, the saccade characteristics were normal for visually guided saccades: The average saccade amplitude was 6.4 dva in both the blank and no-blank conditions (95% confidence intervals, $[5.78$ – $6.87]$ and $[5.78$ – $6.89]$, respectively), and the latencies were 175 [166 – 185] and 177 [168 – 187] ms in the blank and no-blank conditions, respectively.

Performance was better in the blank than in the no-blank condition (lower thresholds in the blank condition, $t = -3.77$; Table 1a), and this did not depend on orientation shift ($t < 1$). There was no interaction between the two factors ($t < 1$). The Bayes factor analysis favored the model including blank as a factor ($BF = 9.5$); there was no or weak evidence in favor of models including orientation shift, both blank and orientation shift, or both factors plus their interaction ($BFs < 1$).

PSE also depended on blank condition ($t = 5.5$), but not on orientation shift, with no interaction between the two factors ($ts < 1$; Table 1b). PSEs tended to be negative in the no-blank

Table 1 Fixed effects, Experiment 1b

	Estimate	SE	<i>t</i> Value
a. Threshold			
(Intercept)	1.01	0.16	6.29
Blank	−0.41	0.11	−3.77
Orientation	0.01	0.01	0.93
Blank × Orientation	−0.01	0.01	−0.83
b. PSE			
(Intercept)	−0.95	0.37	−2.57
Blank	0.86	0.15	5.55
Orientation	−0.01	0.01	−0.81
Blank × Orientation	0.01	0.01	0.63

condition, but not different from zero in the blank condition (Fig. 3c). The Bayes factor analysis favored the model including only blank as a factor ($BF = 23$); there was no or weak evidence in favor of models including orientation shift, both blank and orientation shift, or both factors plus their interaction ($BFs < 1.1$).

Once we had observed this apparent null effect of orientation, we hypothesized that perhaps the shifts were simply too small to be seen or to break object continuity (although this

was not reported by the subjects in postexperiment debriefings or supported by the performance in Exp. 2), and thus we reran the experiment with a large, 45-deg shift.

On average, in Experiment 1c the saccade amplitudes were 6.3 [6.1–6.5] and 6.3 [6.2–6.5] dva, and the saccade latencies were 162 [154–173] and 162 [153–171] ms, for the blank and no-blank conditions, respectively.

Figure 3b shows thresholds in the blank versus the no-blank condition and all four orientation shifts, and Table 2a the fixed effects. Performance was better in the blank condition than in the no-blank condition ($t = -4.3$), and this did not depend on orientation shift ($t < 1$). There was no interaction between the two factors ($t < 1$). The Bayes factor analysis provided evidence in favor of the model including blank as a factor ($BF = 16$); there was no or weak evidence in favor of models that included only orientation shift ($BF < 1$), both blank and orientation shift ($BF = 1.8$), or both factors plus their interaction ($BF < 1$).

The PSEs depended on blank condition ($t = 9.4$), with more negative PSEs in the no-blank condition than in the blank condition (Fig. 3d and Table 2b). There were no effect of orientation shift and no interaction between the two factors ($ts < 1$). The Bayes factor analysis provided strong evidence in favor of the model including only blank as a factor ($BF = 4,883$); weaker evidence in favor of the model including both blank and orientation shift ($BF = 1,280$) or both factors plus their interaction ($BF = 407$); and evidence for the null hypothesis that orientation alone did not influence the PSEs ($BF < 1$).

To compare conditions with and without an orientation shift, we averaged the thresholds across orientation shifts in Experiment 1b and ran an independent Bayesian t test to compare performance between shift and no-shift conditions. The no-shift condition was taken from Experiment 1a. The relevant condition was the no-blank condition, since this was the condition in which we had expected an improvement. The Bayes factor ($BF = 0.36$) favored the null hypothesis that there was no difference in displacement discrimination performance

Fig. 3 Performance (threshold, PSE) in Experiments 1b (a, c) and 1c (b, d). Full circles represent the averages, triangles 95% intervals. Small open circles represent the individual observations

Table 2 Fixed effects, Experiment 1c

	Estimate	SE	<i>t</i> Value
a. Threshold			
(Intercept)	0.62	0.05	12.72
Blank	−0.15	0.04	−4.26
Orientation	−0.0002	0.001	−0.31
Blank × Orientation	−0.0003	0.001	−0.33
b. PSE			
(Intercept)	−0.63	0.21	−2.97
Blank	0.91	0.10	9.40
Orientation	−0.0004	0.002	−0.17
Blank × Orientation	0.0004	0.003	0.14

between shift and no-shift conditions, over the alternative hypothesis that there was.

In sum, Experiments 1b and 1c confirmed the classic blanking effect but provided no evidence that orientation shifts improved displacement discrimination across saccades. To address our hypotheses about the role of features in visual stability, we wanted to probe not only displacement discrimination, but also orientation discrimination. In the second series of experiments, participants no longer reported the direction of displacement, but rather the direction of orientation shift (clockwise or counterclockwise).

Experiment 2a: Orientation shift (report orientation shift)

The aim of Experiment 2a was to determine to what extent the blank influenced performance in reporting a shift in orientation across a saccade. If the blank breaks object correspondence, postsaccadic features might be less likely to mask the presaccadic features, facilitating a comparison.

Method

Subjects Eight healthy human adults (four women, four men; 32 ± 13 years old) participated. All reported normal or corrected-to-normal vision and no oculomotor or neurological impairments, received payment of €10/h for their time, and provided informed consent.

Stimuli and procedure In Experiment 2a, the orientation of the Gabor patch was initialized at 45–135 deg (randomly selected) when it appeared at position *F*. The orientation remained stable as the stimulus stepped from *F* to *T*. When the saccade was in midflight, the patch underwent an orientation shift randomly selected from 18, 9, 6, or 3 deg clockwise or counterclockwise. The new patch appeared either immediately (no-blank condition) or after a 250-ms blank following saccade detection (blank condition). The patch never changed positions during the saccade. Participants were instructed to report whether the change of orientation had been clockwise or counterclockwise, using the keyboard. Each subject performed 512 trials, divided into four blocks of 128 trials each.

We hypothesized that orientation shift discrimination would be better in blank than in no-blank conditions. We also hypothesized that the PSEs would not differ between blank and no blank.

The apparatus and eye movement acquisition were identical to those aspects of Experiment 1a.

Data analyses All data analyses were performed as in Experiment 1, except that the dependent variable was the proportion of “clockwise” responses. The elimination criteria

were also the same as before: trials in which the eye movement was initiated before the appearance of the target (7%) and in which saccade amplitude or latency was more than two standard deviations away from the average ($< 1\%$).

Results

On average, the saccade amplitude was 6.9 dva [6.7–7.1] and the latency was 162 ms [153–171] for both the blank and no-blank conditions.

Figure 4a shows the individual psychometric functions. Discriminating the orientation shift across the saccade did not depend on whether a blank occurred, with average thresholds of 8.0 [5.4–11.0] and 7.5 [5.1–11.0] deg for the blank and no-blank conditions (Fig. 4b). The Bayes factor analysis comparing the hypothesis that performance was better in the blank than in the no-blank conditions to the null hypothesis of equal thresholds between the blank and no-blank conditions revealed evidence in favor of the null hypothesis ($BF = 0.48$).

PSE did not depend on blank, with PSEs of -0.20 [-0.88 to 0.48] in the blank condition and 0.31 [-0.10 to 0.74] in the no-blank condition. Again, the Bayes factor analysis revealed evidence in favor of the null hypothesis of equal PSEs over the alternative hypothesis of different PSEs in the blank than in the no-blank condition ($BF = 0.49$).

In sum, in Experiment 2a we measured transsaccadic orientation discrimination and showed that the irrelevant blank

Fig. 4 (a) Individual psychometric functions in the blank (gray) and no-blank (black) conditions. (b, c) Average (circles) thresholds (b) and PSEs (c), with 95% confidence intervals (triangles). Individual subjects are represented by dashed lines

did not influence performance. However, this did not preclude an influence of an irrelevant displacement on orientation discrimination performance, which was necessary to examine in order to test our hypothesis about the role of visual features and remapping in visual stability. In the next experiment, we thus added an irrelevant intrasaccadic displacement.

Experiment 2b: Displacement and orientation shift (report orientation shift)

Method

Subjects Seven healthy human adults (four women, three men; 31 ± 14 years old) participated. All reported normal or corrected-to-normal vision and no oculomotor or neurological impairments, received payment of €10/h for their time, and provided informed consent.

Stimuli and procedure This experiment was identical to Experiment 1b, except that participants reported the orientation shift (and not the displacement). We hypothesized that performance would be better in conditions with an irrelevant target displacement. The apparatus and eye movement acquisition were identical to those aspects of Experiment 1a.

Data analyses We analyzed performance as in Experiment 2a (threshold, PSE). We tested our hypotheses by performing linear mixed-effect analyses using the lme4 R package (Bates et al., 2015). As fixed effects, we included blank (blank, no blank) and target displacement (± 2 , ± 1 , ± 0.25 dva). The random structure comprised a random intercept by subject. We eliminated trials as before: trials in which the eye movement was initiated before the appearance of the target (7%) and in which the saccade amplitude or latency was more than two standard deviations away from the average ($< 1\%$).

Results

On average, the saccade amplitudes were 6.7 [6.6–6.9] and 6.7 [6.5–6.9] dva, and the latencies were 162 [152–172] and 162 [153–172] ms in the blank and no-blank conditions, respectively.

Figure 5a shows the thresholds for blank versus no-blank conditions and all six target displacements, and the fixed effects are in Table 3. Performance depended marginally on blank ($t = 2.06$), and not on displacement ($t < 1$). There was no interaction between the two factors ($t < 1$). The Bayes factor analysis revealed evidence in favor of the null hypothesis (absence of a difference in thresholds) over models that included blank, displacement, and their interaction (all BFs < 1).

PSE did not vary with blank or displacement, or with their interaction (t s < 1 ; Fig. 5b and Table 3b). The Bayes

Fig. 5 Performance in Experiment 2b: threshold (a) and PSE (b). The conventions are as in Fig. 3

Table 3 Fixed effects, Experiment 2b

	Estimate	SE	<i>t</i> Value
a. Threshold			
(Intercept)	6.61	1.38	4.80
Blank	0.82	0.40	2.06
Displacement	0.03	0.24	0.11
Blank $\times$ Displacement	0.04	0.34	0.13
b. PSE			
(Intercept)	-0.15	0.42	-0.35
Blank	0.26	0.29	0.91
Displacement	-0.14	0.17	-0.80
Blank $\times$ Displacement	0.03	0.24	0.13

factor analysis revealed evidence in favor of the null hypothesis (absence of a difference in PSE between blank and no blank) over models that included blank, step, and their interaction (all BF_s < 1).

We compared performance between no displacement (Exp. 2a) and displacement (Exp. 2b) conditions in the no-blank version of the task. We averaged the thresholds across displacements in Experiment 2b and ran an independent Bayesian *t* test to compare performance between displacement and no-displacement conditions. The Bayes factor (BF = 0.41) favored the null hypothesis of no difference in orientation discrimination performance between displacement and no displacement, over the alternative hypothesis of a difference.

Discussion

In a modified version of the in-flight displacement task, we replicated classic SSD findings. Discrimination thresholds for the direction of the intrasaccadic target displacement were lower when a ~250-ms blank separated the end of the saccade and the appearance of the displaced target than when the displaced target was immediately visible after the saccade. We also found that in the no-blank condition, PSEs were negative: A stable target was perceived to have stepped forward, and stability was perceived for a target stepping backward. In the blank condition, this bias disappeared.

These findings reflect the importance of the spatiotemporal correspondence between the predicted postsaccadic location of the target and its actual location (Deubel, 2004). Points of subjective equality are a measure of the gain of the CD signal. Imagine a saccade target at 8 dva. In the case of a perfect 8-dva saccade with a CD with a gain greater than 1, then the predicted location of the postsaccadic target would be negative; that is, according to the internal copy of the saccade, the eyes would land beyond the target. However, because the saccade actually landed exactly on the target, there was a mismatch between the predicted and actual locations of the postsaccadic target, and subjects reported that the target had stepped backward. Stability would be perceived if the target stepped backward to match the overestimated gain. Thus, in our data, the negative PSEs suggest a CD gain greater than 1. In the blank condition, PSEs shifted back to zero, suggesting that the gain of the CD signal no longer played a role in determining the response. Rather, performance was determined by accurate location signals.

Contrary to our hypotheses, spatiotopic performance (displacement discrimination thresholds) did not improve with the addition of an irrelevant orientation shift (although the effect of the blank was still present with these shifts). We checked that this was not due to the fact that our orientation shifts were too small to be perceived, in three ways: We reran the experiment with very large shifts (45 deg) and replicated the null

result (Exp. 1c); we asked participants in a postexperiment debriefing whether they had perceived the shifts (they did, and easily); and we measured perception in a second series of experiments (our large shift levels were well above threshold). Our result was in contrast to several previous studies showing that irrelevant feature changes across saccades can improve displacement discrimination. Demeyer et al. (2010) switched shape (e.g., square to triangle) and found that spatiotopic performance was better than in the no-switch control. Tas et al. (2012) switched contrast polarity (white to black) and object identity (e.g., button to clock) and also reported that performance was improved in conditions with an irrelevant feature change. In these studies, blanking and feature changes were manipulated in separate trials, not simultaneously as in the present experiments. Although it is an empirical question whether such a small methodological difference could cause the large difference in the pattern of results, we cannot imagine a reasonable hypothesis as to why this would gate the influence of feature changes on spatiotopic performance. Zimmermann, Born, Fink, and Cavanagh (2014) switched a single bar from left-oriented to right-oriented, and this shape/orientation shift also improved performance. However, orientation shifts of a single bar also modify location signals. We had therefore expected orientation shifts to relieve SSD; our negative results suggest that not all visual features contribute to object continuity across saccades.

In the second series of experiments, we asked participants to report whether the feature underwent a change across the saccade, by asking them to report the orientation shift and ignore any displacements. Subjects were able to perform the task, but none of our experimental manipulations influenced their performance: neither the blank nor the displacement. Again, this contrasts with previous reports suggesting that a blank improved transsaccadic detection of form (Deubel et al., 2002), color (Tas et al., 2014), or spatial frequency (Weiß, Schneider, & Herwig, 2015).

In a related set of studies, Schneider and colleagues showed that changing the surface features of the target object across the saccade deteriorated postsaccadic object recognition (measured by the identification of a letter embedded within the postsaccadic object), relative to a condition in which the surface features of the object remained the same across the saccade (Poth & Schneider, 2016). Poth, Herwig, and Schneider (2015) showed that a blank improved displacement discrimination (the classic blanking effect), but that it deteriorated letter identification. These results were interpreted as suggesting that when pre- and postsaccadic objects are considered two distinct objects, they may compete for attention, leaving fewer resources available for the letter identification task (Schneider, 2013). In our study, we did not ask participants to report the orientation of the postsaccadic object independently from the presaccadic orientation (we asked them to report the direction of change between the two), so we cannot

directly address this idea of competing representations between the pre- and postsaccadic objects. However, competition between representations may degrade performance in the comparison between pre- and postsaccadic objects, leading to higher thresholds in the blank condition. We did not replicate this finding with our orientation task, since the blank had no effect on orientation discrimination of the postsaccadic object. There are several possible sources for this difference. First, Poth et al. (2015) did not actually test postsaccadic object perception, but perception of a letter within the object. It is not mutually exclusive to have deteriorated letter identification and normal object identification. Second, letter identification taps into processes that are probably quite different from those involved in orientation discrimination.

Our results do not provide unequivocal support for either account of visual stability: remapping or VSTM. The VSTM account of visual stability predicts that changing the orientation should unmask target displacements, but we found no effect of orientation shifts on displacement discrimination. The remapping account of visual stability predicts that displacing the target should unmask feature changes, but we found no effect of displacements on orientation discrimination. It also predicts an improvement in performance with a blank, which again we did not find. We do not believe that this is due to the displacements being too small to be perceived, because we asked participants in a postexperiment debriefing whether they had perceived any displacements (they did), and we measured that perception in the first series of experiments (our large displacements were well above threshold). Perhaps our orientation shifts were too easy to discriminate, leading to a ceiling effect. We think this is unlikely: First, the discrimination thresholds measured in the no-displacement condition (Exp. 2a) were higher than some of the tested shifts. Also, even in the subjects with high thresholds, in which there may have been room for improvement, the blank did not change performance.

We are thus left with evidence in the literature, and in the present results, of the importance of spatiotemporal information about the predicted postsaccadic location of the target, arguing in favor of remapping as a crucial mechanism for visual stability. We also have evidence in the literature, but not in the present results, of the importance of retaining feature information across saccades for visual stability. We conclude that both mechanisms must play a role for visual stability—that is, spatiotemporal knowledge both about the saccade, in the form of a CD signal, and about the visual attributes of the target. Our results suggest that not all visual features are taken into account to establish object continuity and visual stability. In particular, orientation does not play the same role as shape or polarity. A fascinating question for future research will be to map out which visual features do serve visual stability and which do not—and why.

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