Orthogonal steps relieve saccadic suppression

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Although the retinal position of objects changes with each saccadic eye movement, we perceive the visual world to be stable. How this visual stability or constancy arises is debated. Cancellation accounts propose that the retinal consequences of eye movements are compensated for by an equal-but-opposite eye movement signal. Assumption accounts propose that saccade-induced retinal displacements are ignored because we have a prior belief in a stable world. Saccadic suppression of displacement—the fact that small displacements of the visual targets during saccades go unnoticed—argues in favor of assumption accounts. Extinguishing the target before the displacement unmasks it, arguing in favor of cancellation accounts. We show that an irrelevant displacement of the target orthogonal to saccade direction unmasks displacements parallel to saccade direction, and therefore relieves saccadic suppression of displacement. This result suggests that visual stability arises from the interplay between cancellation and assumption mechanisms: When the post-saccadic target position falls within an elliptic region roughly equivalent to habitual saccadic variability, displacements are not seen and stability is assumed. When the displacements fall outside this region, as with our orthogonal steps, displacements are seen and positions are remapped.

Introduction

The perception of a high-resolution visual world depends on saccadic eye movements that bring different parts of the visual scene onto the fovea. However eye movements also challenge visual perception, because the retinal image of an object shifts with each saccade. Nevertheless, we do not experience the world as continually jumping; rather, we have the impression of a visually stable world, and have at least some spatial representations that are independent of the constant retinal shifts. How this stability arises is a matter of debate, and, broadly speaking, there are two families of explanations.

According to one type of explanation, presaccadic positions are remapped to postsaccadic coordinates in an active process of compensation that allows the visual system to discount the effects of its own eye movements and to represent positions and displacements in a spatiotopic reference frame. According to the second type of explanation, no active compensation is necessary because we assume that the world is stable unless given overwhelming evidence to the contrary. We will call these two types of explanation "calculation" and "assumption," respectively.

According to "calculation" explanations of stability, retinal jumps due to eye movements are canceled by mapping retinal coordinates to some sort of spatiotopic map, or at least remapping presaccadic object positions to their expected postsaccadic coordinates. Both kinds of mapping require information about eye position, and this information is usually assumed to come from the efference copy of the eye movement command (Helmholtz, 1924; Sperry, 1950; von Holst & Mittelstaedt, 1950). Such explanations are bolstered by neurophysiological findings that show predictive changes in visual maps prior to eye movements (Duhamel, Colby, & Goldberg, 1992) and efference copy circuits whose deactivation impedes the updating of sensorimotor maps (Sommer & Wurtz, 2002, 2006)—see Wurtz (2008) for a review. However, investigations of efference copy have shown it to be imperfect: It is slower than the eye movement (Matin & Pearce, 1965) and smaller in amplitude (Grüsser, Krizič, & Weiss, 1987). Any discrepancy between the actual eye position and that signaled by efference copy should lead to a breakdown of visual stability, but this hardly ever occurs. Therefore, "calculation" explanations cannot account for all of visual stability.

In contrast, "assumption" explanations hold that the visual system posits the null hypothesis or prior of a stable world, and requires strong evidence to perceive

object motion during eye movements (Bridgeman, Van der Heijden, & Velichkovsky, 1994; Gibson, 1966; MacKay, 1958; O'Regan, 1992). There is evidence that the postsaccadic position of the saccade target serves as an anchor to link pre- to postsaccadic coordinates (Currie, McConkie, Carlson-Radvansky, & Irwin, 2000; Deubel, Bridgeman, & Schneider, 1998).

The phenomenon of saccadic suppression of displacement (Bridgeman, Hendry, & Stark, 1975; Mack, 1970; Wallach & Lewis, 1966) provides evidence for both types of mechanisms. When a visual stimulus, usually the saccade target, is displaced in the same direction as the saccade, and in a time window that begins about 50 ms before the saccade and ends shortly after the end of the saccade, displacements as large as 10%–30% of the saccade amplitude are not perceived and their directions cannot be discriminated. This large tolerance for displacements seems to support "assumption" explanations of stability, but the fact that even larger displacements *can* be seen seems to require a mechanism beyond a mere assumption of stability.

The existence of two separate mechanisms is highlighted by a phenomenon discovered by Deubel, Schneider, and Bridgeman (1996), called the *temporal blanking effect*. In a modification of the usual saccadic suppression paradigm, the target disappears during the saccade, but instead of reappearing immediately at a new location, reappears at the new location after a temporal blank lasting 50–250 ms after saccade offset. Performance in judging whether the target stepped forwards or backwards improves dramatically for blank durations over 200 ms or so: psychometric slopes increase, and biases move closer to zero (Deubel, Schneider, & Bridgeman, 1996). This result is surprising because the temporal blank introduces no new geometrical information—yet performance increases markedly. This seeming paradox has led Deubel and his coauthors to propose a dual-mechanism explanation: Without the blank, on one hand, the saccade target is immediately located and assumed to be the same object and in the same location as the pre-saccadic stimulus. The blank, on the other hand, leads the visual system to assume that the target is a new object, and to use all signals, including efference copy, to calculate the expected target location, rather than to simply assume that the target hasn't moved (Deubel, 2004; Deubel, Bridgeman, & Schneider, 1998). More recently, it has been found that changing the target's shape can also lead to increases in trans-saccadic localization performance, similarly to the temporal blanking effect (Demeyer, De Graef, Wagemans, & Verfaillie, 2010).

In the present study, we show that another way to alleviate saccadic suppression, without adding any additional information, is to add an irrelevant orthogonal step. Thus, during the saccade, the target steps diagonally. The subject's task is to discriminate the direction of the component of the step *parallel* to the saccade. The component of the step *orthogonal* to the saccade is irrelevant and non-informative, yet is found to increase performance, or to relieve saccadic suppression, as much as the temporal blank.

Methods

Apparatus

Stimuli were displayed on a Sony GDM-F520 CRT set to video mode 800×600 with refresh rate 150 Hz. The display area was 38.5×29 cm. Eye movements were measured with the EyeLink 1000 eye tracker (SR Research Ltd., Mississauga, Ontario, Canada) operated in monocular mode at 1000 Hz, with data filtering off for lower latency response. The mean latency in the eyetracker-computer-display system was about 10 ms (1.5 monitor frames in double-buffered mode) plus about 3 ms of eyetracker latency.

Participants sat approximately 57 cm from the monitor, with their head movements restrained using the EyeLink chin- and headrest. Other than the light emitted by the CRT monitor, the experimental room was dark.

Stimuli and procedure

The geometry of the stimuli is illustrated in Figure 1. Lengths and sizes will be given in centimeters, with 1 cm approximately equal to 1° of visual angle. All stimuli were black squares (size 0.5 cm) drawn on a uniform gray (40 cd/m^2) background. We used stimuli darker than the background in order to have the fastest possible offset, so as to avoid any issues with monitor persistence. Each trial began with a fixation point (labeled "F" in Figure 1), located in a randomly chosen position in a 6 cm square area centered on the monitor. The fixation point was displayed for a random duration between 750 and 1500 ms. At offset, it was immediately replaced by the saccade target ("T" in Figure 1), located 6 or 8 cm to the left or right. This was the signal for the participant to perform a saccade to the target.

At target onset, initial gaze position was recorded. Saccades were detected on-line using the following simple threshold criterion: Saccade onset was said to have occurred when the horizontal component of gaze differed by more than 2 cm from the initial gaze position in the direction of the required eye movement. At saccade onset, the target disappeared and either immediately reappeared in one of the 18 positions shown in red and blue in Figure 1, in the *no-temporal-blank* condition, or reappeared in the new position after
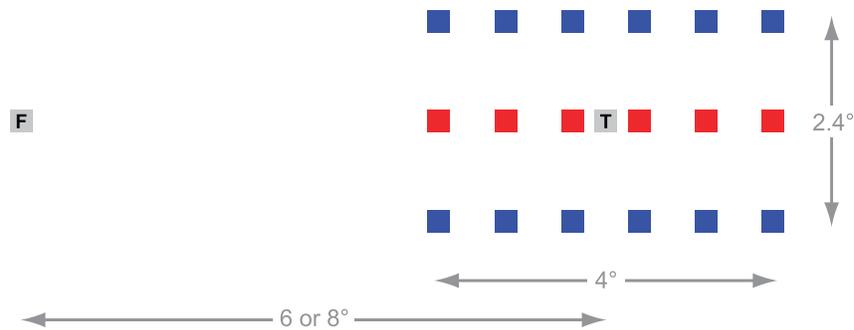
Figure 1. Schematic description of stimuli, showing an example of a trial with a rightward saccade. Initially, a fixation point (F) is displayed. The fixation point is replaced by a target (T), 6° or 8° to the right or left of the fixation point. When a saccade to the target is detected, the target disappears and is replaced, either immediately (no temporal blank condition) or 200 ms later (temporal blank) by an identical stimulus at one of the 18 final locations shown in red or blue. (All stimuli are the same color; the colors in this diagram are for descriptive purposes.) The six red locations are the no-vertical-step condition; the 12 blue locations are the vertical-step condition. The subject's task is to report the horizontal direction of the final target step: The correct response for the nine final locations on the left of target T is "left," and "right" for the nine locations on the right. Thus, the vertical step is irrelevant to the task, adding no additional information to the horizontal step.

a 200 ms temporal blank (*temporal-blank* condition). The target could step either only horizontally, i.e., parallel to the saccade, in the *no-orthogonal-step* condition, shown by red targets in Figure 1; or have an additional orthogonal component (*orthogonal-step* condition), as shown by the blue targets in Figure 1. In either case, the target remained in its new position for 600 ms before disappearing. The participant then reported whether the *horizontal* component of the target step had been to the left or right by pressing the left or right mouse button. Participants were instructed to ignore any vertical component of the target step, which, from the point of view of the task, was irrelevant and uninformative.

The experiment was carried out in a randomized factorial design, with 2 saccade directions × 2 saccade amplitudes × 6 parallel target steps (−2.0, −1.2, −0.4, +0.4, +1.2, +2.0) × 2 orthogonal step amplitudes (0, 1.2) × 2 orthogonal step directions (no effect for 0 amplitude) × 3 repetitions, yielding 384 trials per participant. Prior to the main block, participants performed 20–30 practice trials, to get accustomed to performing the saccade and the perceptual task. During the main block, there was a pause every 64 trials, following which the eye tracker was calibrated using the standard 9-point EyeLink procedure.

Participants

Sixteen unpaid volunteers participated in the experiment, after giving informed consent; many were experienced psychophysical observers, but all except three were naïve as to the purposes of our study. All had normal or corrected-to-normal vision, and no known neurological deficits.

Results

The data of three participants were removed from subsequent analysis because each had a point of subjective stationarity (PSS) that lay outside the range of horizontal steps in at least one condition. The eye movements of the remaining participants were analyzed in order to eliminate trials in which the oculomotor task wasn't adequately performed. Saccades were identified using the default EyeLink criteria (velocity threshold of 30°/s, acceleration threshold of 9500°/s^2). We first eliminated trials in which, during the period from 50 ms prior to the go signal to 50 ms past the appearance of the target at the final position (the "critical period"), there were any blinks, or more than one saccade (excluding microsaccades, defined as having amplitude below 1 cm). The remaining trials had precisely one saccade with amplitude above 1 cm in the critical period, which we will call the "main saccade." Saccadic error was defined as the vector difference between the main saccade and the target saccade corresponding to the initial target displacement, (±6, 0) or (±8, 0). We eliminated trials in which saccadic error was above 3 cm horizontal or 1 cm vertical. In total, we eliminated about 9.6% of all trials. The fractions of eliminated trials in all four conditions, as well as saccade metrics in the remaining trials, are shown in Table 1. As expected (because the differences between the conditions apply only after the saccade begins), and as can be seen in the table, there are no substantial differences between the conditions.

Responses to the displacement discrimination task were coded as +1 for perception of forward target displacement (with respect to the direction of the saccade) and −1 for backward. These responses were

Absolute vertical step (cm)	Temporal blank (ms)	Eliminated trials	Horizontal saccadic error (cm)	Vertical saccadic error (cm)	Saccade latency (ms)
0	0	9.4%	−0.37 [0.74]	0.13 [0.29]	161 [39]
1.2	0	9.4%	−0.37 [0.77]	0.13 [0.29]	163 [46]
0	200	9.6%	−0.34 [0.72]	0.14 [0.31]	163 [45]
1.2	200	10.0%	−0.36 [0.73]	0.13 [0.30]	164 [41]

Table 1. The percentage of eliminated trials, saccadic errors, and saccadic latencies in the four conditions. Saccadic errors were defined as if the saccade were to the right, so that negative horizontal errors denote undershoot. Standard deviations are given in brackets.

fitted as logistic functions of target displacements, namely

$$R(x) = -1 + 2/\left[1 + e^{-k(x-x_0)}\right],$$

where x was the target displacement parallel to the saccade and $R(x)$ the predicted response (whose signs were defined as positive when in the same direction as the saccade, and negative when opposite), x_0 the bias, and k the slope. Fits were performed using maximum likelihood estimation, with a prior disfavoring high slopes of the logistic function shaped like a third-order Butterworth filter,

$$p(k) = 1/\sqrt{1 + (k/k_0)^6},$$
$$\text{with cutoff } k_0 = 0.1 \text{ cm}^{-1},$$

in order to deal with aliasing due to the discrete distribution of horizontal steps. Examples of data from a representative subject and corresponding fits are shown in Figure 2a and b. Fits were performed separately for each participant and each of the four conditions. In all cases, a maximum value of the log-likelihood was found, starting from the initial values $x_0 = 0$, $k = 1$. Furthermore, the R^2 goodness-of-fit measure (or coefficient of determination) was positive in all cases, with mean value 0.49 and standard deviation 0.20.

As can be seen for the participant in Figure 2, in the no-temporal-blank condition the slope of the psycho-metric curve is lowest in the no-orthogonal-step condition, and noticeably higher for orthogonal steps. In the temporal-blank condition, on the other hand, both slopes are rather high, and there seems to be little effect of the orthogonal step. We transform the slopes to thresholds, defined as the distance from the point of subjective stationarity (PSS) to performance at 75% correct. We express thresholds as Weber fractions, by dividing them by 7°, the mean required saccadic amplitude. We first fit the data separately for leftward and rightward saccades, and for 6° and 8° saccades. We found no effect of either direction or amplitude on PSSs or thresholds (using Mann-Whitney tests to compare means, Brown-Forsythe tests to compare variances, and Kolmogorov-Smirnov tests to compare

distributions, corrected for multiple tests). Therefore, in all subsequent analyses we collapsed the data for the two directions and amplitudes.

Thresholds for all participants in all four spatio-temporal conditions are shown in Figure 3a, along with between-subject means and confidence intervals. As can be seen in that figure, in the no-temporal-blank condition the orthogonal step leads to lower thresholds in all participants. Indeed, mean threshold without the orthogonal step was 0.181, while with the orthogonal step it was 0.091. A Mann-Whitney test showed that thresholds were significantly lower with the orthogonal step ($U = 148$, $p = 0.001$). (We did not use t tests because threshold distributions were significantly non-normal.) The temporal blank, in the absence of the orthogonal step, also lowered thresholds, to a mean of 0.073, and this difference was significant ($U = 162$, $p < 0.0001$). However, none of the other contrasts was significant when correcting for multiple tests. In particular, there was no significant difference between the temporal-blank and orthogonal-step conditions, nor was there an effect of adding the temporal blank to the orthogonal step, nor of adding the step to the blank.

The points of subjective stationarity (PSS), as determined from our fits, are shown in Figure 3b. Values in Figure 3 correspond to the signed PSSs, but to determine whether performance improved between our conditions we compared the absolute values of the biases. PSSs were significantly closer to zero with the vertical step than without, when there was no temporal blank (mean absolute values 0.50 and 1.10, respectively; $t_{12} = 4.99$, $p < 0.001$). In the temporal blank condition, there was no significant difference between mean absolute PSSs (0.68 with the vertical step and 0.73 without).

Instead of remapping or compensating target posi-tion for eye movement, subjects could simply respond based on target retinal position at the end of the saccade: If the target's horizontal position is to the right of the fovea, respond "right"; otherwise respond "left." Following a report by Collins, Rolfs, Deubel, & Cavanagh (2009) that this simple strategy was *not* used, we wished to check this question in our current data, using a somewhat different analysis. The position of the
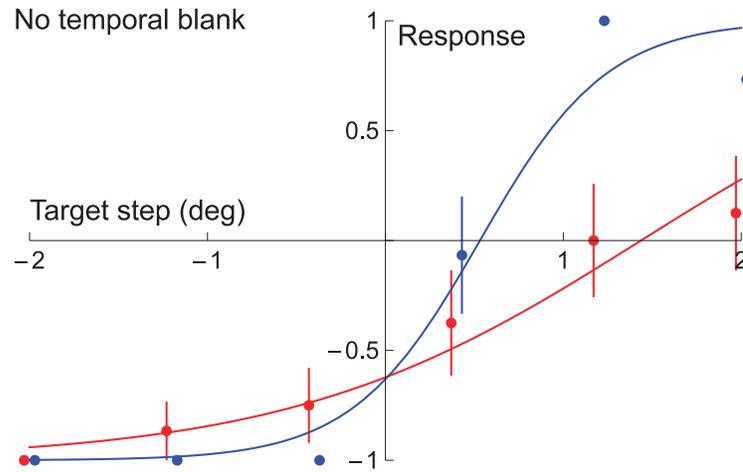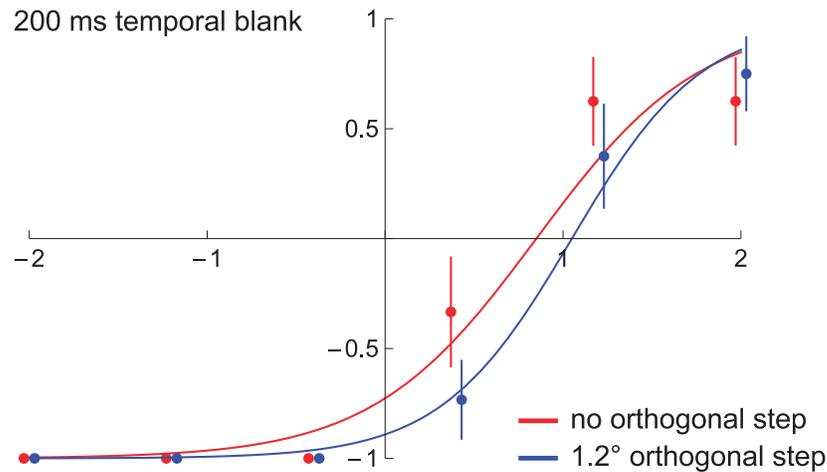
Figure 2. Data for one representative subject (a) for no temporal blank and (b) temporal blank condition, each showing data for no vertical step (red) and vertical step (blue) conditions. Points show mean response as a function of horizontal step. For rightward saccades, rightward steps are coded as positive, and rightward responses as +1; leftward steps as negative, and leftward responses as −1. For leftward saccades, the signs are reversed, so that positive numbers denote forward displacements and responses (with respect to the direction of the main saccade), and negative backward. Points show mean responses, and error bars are standard errors. Curves show the resulting logistic fits.

target on the retina after its final displacement is the sum of two terms: the target's step, and the subject's saccadic error. The analysis thus far has only taken the target step into account. The distribution of saccadic errors, combined across all conditions and participants, is shown in Figure 4. We expanded our logistic analysis to include saccadic error as a second independent variable, fitting responses R_i on trial i to $\sigma(s_i + be_i, x_0, k)$, where s_i is the final horizontal step on trial i, e_i the horizontal component of saccadic error, and $\sigma(\cdot\ x_0, k)$ the logistic function with PSS x_0 and slope k. If the coefficient b is 1, this is a sign that the retinal strategy is being used, because responses are based on retinal

position; if b is 0, on the other hand, then responses are independent of retinal error, and therefore based on the target step in an eye-independent reference frame. Performing the two-dimensional logistic fit independently for each subject in each of the four conditions, we found only one case out of 52 in which b was significantly different from 0, but in this case it was *negative* (no-temporal-blank-no-orthogonal-step condition, $b = -0.79$, $p < 0.001$; parametric bootstrap, Bonferroni correction for multiple tests). The means of the b coefficients across subjects were −0.04, +0.07, −0.10, and +0.18 in the no-temporal-blank-no-orthogonal-step, no-temporal-blank-orthogonal-step, tempo-
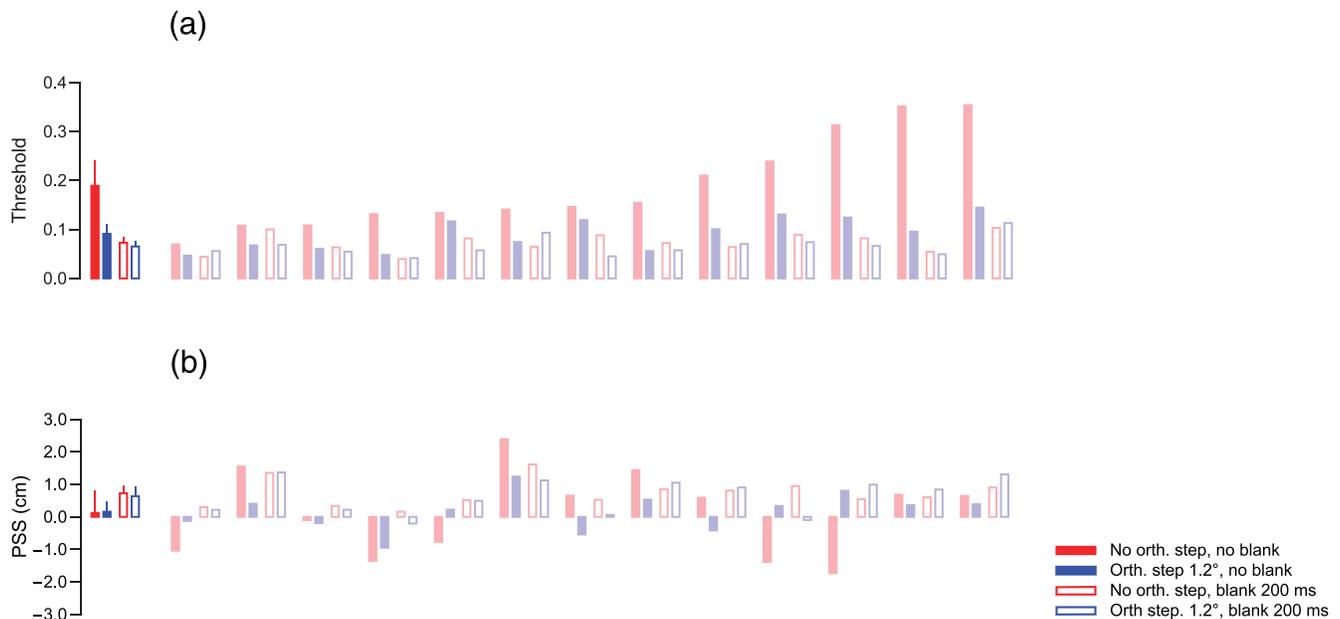
Figure 3. (a) Thresholds (expressed as Weber fractions relative to saccade amplitude) and (b) PSSs (expressed in cm, with 1 cm approximately equal to 1° of visual angle) for individual subjects in the four conditions (dim bars on the right), and means in each condition across subjects (bright bars on the right). Error bars show between-subject 95% confidence intervals.

ral-blank-no-orthogonal-step, and temporal-blank-orthogonal-step conditions, respectively, and none was significantly different from 0 (*t* tests). Thus, in agreement with Collins et al. (2009), but using different analyses, we confirm that responses for target displacement were not based on retinal position.

We wanted to check whether there was any relation between saccadic metrics and task performance, and in particular if thresholds were positively correlated with the variance of saccadic error in the direction of the saccade (i.e., the more variable the saccade landing position, the higher the threshold), as reported by Niemeier, Crawford, and Tweed (2003). We found that, on one hand, the between-subject correlation coefficients between these variables were 0.35 and 0.56 in the no-temporal-blank-no-orthogonal-step and no-temporal-blank-orthogonal-step conditions, respectively, and that both of these correlations were significantly above 0 (non-parametric bootstrap). On the other hand, the correlations were 0.33 and 0.17 in the temporal-blank-
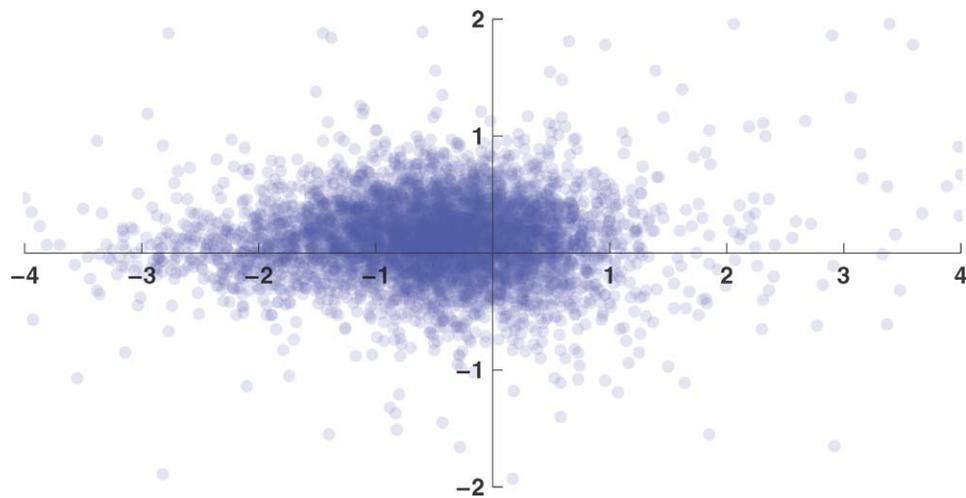

Figure 4. Distributions of saccadic errors across all conditions and subjects, expressed in centimeters, with 1 cm approximately equal to 1° of visual angle. Leftward and rightward saccades were combined by multiplying the horizontal component of leftward saccades by −1. For our analyses, we removed trials in which saccadic error was above 3 cm horizontal or 1 cm vertical.

no-orthogonal-step and temporal-blank-orthogonal-step conditions respectively, with a non-parametric bootstrap showing that neither one differed significantly from 0.

Discussion

Our results show that task-irrelevant orthogonal target steps during a saccade unmask displacements along the saccade axis that otherwise go unnoticed. We also replicate both the classic saccadic suppression of displacement (our no-temporal-blank, no-orthogonal-step condition; Bridgeman, Hendry, & Stark, 1975) and the temporal blanking effect (Deubel, Schneider, & Bridgeman, 1996) and additionally show that the orthogonal-step and temporal-blanking effects are not additive. Indeed, the relief from saccadic suppression due to the temporal blank is comparable to the relief due to the orthogonal step, and no additional performance gain occurs when the blank and the step co-occur.

Our effect should not be confused with the finding that saccade-orthogonal displacements are detected with much lower thresholds than saccade-parallel displacements (Mack, 1970; Niemeier et al. 2003). In our study, we always measured thresholds for detecting saccade-*parallel* displacements, accompanied or not by task-irrelevant and uninformative orthogonal steps.

Why would task-irrelevant, uninformative orthogonal steps relieve saccadic suppression of saccade-parallel displacements? Consider the localization problem that the visual system faces after each saccade. The retinal image shifts by an amount equal-and-opposite to the saccadic vector, which—due to saccadic error—is different from the vector from the initial fixation point to the saccade target. During the saccade, objects, and in particular saccade targets may also move. (Although saccades are fast, they are also frequent, and therefore occupy probably 10%–20% of our waking life; quite a bit of motion may take place during that time.) The two motions—due to eye movement and object movement—add to produce a compound displacement on the retina.

An important task for the visual system is to tell if the displacement on the retina of an object, say the saccade target, across a saccade was due to eye movement alone, or to a combination of eye movement and object movement. A way to make this distinction would to make use of the distribution of motor errors. Saccadic errors—as can be seen in Figure 4—are not isotropic, but distributed approximately as an ellipse, elongated in the direction of the saccade (van Opstal & van Gisbergen, 1989). A reasonable assumption would be that if, on one hand, after the saccade the target falls

within such an ellipse about the fovea, then the target has not moved during the saccade: the null hypothesis of world stability (Bridgeman, Van der Heijden, & Velichkovsky, 1994; MacKay, 1958). Under this stability assumption, target motion on the retina is due to eye movement alone, and its postsaccadic position off the fovea is due to motor error. Indeed, if the saccade target does fall in the elliptic error region, and no independent motion is assumed, the visual system anchors the postsaccadic reference frame on the target's actual retinal position (Deubel, Bridgeman, & Schneider, 1998).

If, on the other hand, the target falls outside the error ellipse, then the visual system could reasonably assume that the target has moved independently. In our case, an orthogonal displacement of 15%–20% of the saccade amplitude is apparently large enough to exit the ellipse in the direction of its minor axis and to unmask previously undiscriminable parallel displacements. With the orthogonal step, the null hypothesis of stability no longer seems to be made, and other signals seem to be driving localization judgments. These signals are most likely efference copy and, possibly, proprioception, as shown by our observation that localization judgments are independent of saccade error, and therefore depend on the actual, trial-by-trial saccade amplitudes (Collins et al., 2009).

With the orthogonal step, the subjective impression spontaneously reported by many observers is that of clear apparent motion, much clearer than without the orthogonal step. Since the initial stimulus of the apparent-motion pair (the saccade target) is seen before the saccade, and the final one after the saccade, this is an example of trans-saccadic apparent motion. As recently shown by Szinte and Cavanagh (2011; see also Rock & Ebenholtz, 1962), trans-saccadic apparent motion is largely spatiotopic. This is also the case in our data, as shown by biases in the orthogonal-step condition being close to zero. The orthogonal step leads to a clear impression of diagonal motion; its horizontal component can be effortlessly "read off" to extract the direction of the horizontal displacement in order to perform the task. Paradoxically, this clear and accurate trans-saccadic mapping, whose underlying signals must always be present, seems to be inaccessible to the observer without the orthogonal step (or without the temporal blank: see Deubel et al., 1996).

Thus, we postulate that the saccade-error ellipse, with its major axis in the direction of the saccade, plays a crucial role in trans-saccadic visual stability. If the saccade target is located within this ellipse, stability is *assumed*, leading to strong saccadic suppression of displacement; if the target lies outside, efference copy is used to accurately *remap* presaccadic locations to the postsaccadic reference frame. The transition between the "assume" and "remap" regimes may of course be

gradual: Future studies should characterize its functional dependence on stimulus and saccade metrics.

The model may be extended to the temporal dimension. The stability ellipse may shrink and disappear over a period of several hundred milliseconds, resulting in the temporal blanking effect (Deubel et al., 1996). Objectively, the effects of the orthogonal step and the temporal blank are very similar and statistically indistinguishable in our data. Moreover, the combination of orthogonal step and temporal blank does not lead to more precise localization judgments than either one alone, leading us to suspect that the two manipulations activate the same mechanism. Subjectively, similarly clear apparent motion is perceived with either the temporal blank or the orthogonal step or both, but not when the two are absent. The recent finding that shape change also relieves saccadic suppression of displacement (Demeyer et al., 2010) shows that other, more abstract dimensions, such as that of shape, may also be incorporated in this model. Indeed, we may wonder whether a noticeable change in any stimulus dimension (or even a subthreshold change) will lead to relief from saccadic suppression of displacement.

An alternative explanation of the relief from saccadic suppression provided by temporal blanking is that the extraretinal signal, which evolves slower that the eye movement itself (Matin, 1972), may simply be more precise and accurate several hundred milliseconds after the saccade than immediately following the saccade (Deubel et al., 1996). The orthogonal step effect demonstrated here, and its similarity to the temporal blanking effect, as well as the effect of target shape change shown by Demeyer et al. (2010), show that this alternative explanation is probably invalid. Indeed, our results show that relief from saccadic suppression is available immediately following the saccade. Thus, there really do seem to be two separate regimes, in which either the saccade target is found in the appropriate spatio-temporal window with the appropriate shape—and then its stability is assumed—or it is not, and its pre-saccadic position is remapped using efference copy signals.

Thus, we find an interplay between two contrasting mechanisms of visual stability: on one hand the *assumption* that the world is stable during eye movements, and on the other hand the *calculation* or remapping of post-saccadic coordinates of pre-saccadic objects, possibly leading to spatiotopic representations. The two mechanisms are complementary: the assumption provides the impression of stability (yielding false negatives for independent object motion), whereas the calculation provides predicted object positions (yielding false positives when these predictions are inaccurate). The orthogonal step effect shows that the transition

between these mechanisms can occur not only at temporal but also at spatial limits.

Acknowledgments

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