

Post-saccadic location judgments reveal remapping of saccade targets to non-foveal locations

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The present study addresses the question of how objects are localized across saccades. In a task requiring participants to compare the location of a post-saccadic probe with the pre-saccadic target, we investigated the roles of saccade landing site and post-saccadic probe location. Saccade landing sites vary from trial to trial because of oculomotor error but can also be shifted by saccadic adaptation. Visual targets were extinguished during the saccade and reappeared after a short blank to counteract saccadic suppression of displacement. Performance in localizing targets after unadapted saccades was nearly veridical and independent of actual landing site, showing that trial-to-trial oculomotor error did not contribute to post-saccadic localization. This result suggests that much of the oculomotor error of saccades is included in the efference copy vector and this allows the recovery of a remapped target location that is often not foveal, but stable and accurate across trials. Displacement judgments relative to this remapped location will be independent of trial-to-trial variability in landing site. After adapted saccades, post-saccadic localization shifted in the direction opposite to adaptation but again, trial-by-trial landing site variability did not correlate with performance. This result suggests that the efference copy matches the planned upcoming saccade, be it adapted or not.

Keywords: eye movements, spatial vision, visual cognition

Citation: Collins, T., Rolfs, M., Deubel, H., & Cavanagh, P. (2009). Post-saccadic location judgments reveal remapping of saccade targets to non-foveal locations. *Journal of Vision*, 9(5):29, 1–9, <http://journalofvision.org/9/5/29/>, doi:10.1167/9.5.29.

Introduction

Saccades pose a challenge to visual localization and therefore offer a number of insights into how the visual system codes location. Indeed, every saccade induces a brief break in the ongoing acquisition of visual information and changes the retinal location of objects from one fixation to the next. To study the coding of visual location, it is possible to remove a saccade target while the saccade is in mid-flight, that is, before the eyes land, and have it reappear at the same or another location after the saccade. What determines the perceived location of such a probe relative to the location of the pre-saccadic target? If the saccade is accurate, it should end on the target's pre-saccadic location and the probe's displacement ought to be judged relative to saccade landing site. However, saccades are not exact and some of their error may be predicted from the efference copy of the motor command

(Bridgeman, 1995); subtracting this efference copy vector from the saccade vector provides information about where the target should be when the saccade lands—the target is thus remapped to its expected post-saccadic retinal location, correcting for much of the oculomotor error (Figure 1). If this remapped location is used to judge a probe's displacement relative to the original target, the displacement judgments would be independent of the actual landing site. Alternatively, if the efference copy does not include trial-by-trial oculomotor variability, displacement judgments should vary with landing site. To compare these two alternatives, we analyzed displacement judgments of probes presented about 200 ms after saccade landing to determine the role of trial-by-trial landing locations for both normal and adapted saccades.

Judging relative displacement between pre- and post-saccadic target locations is known to be very difficult if the saccade target is displaced when the saccade is in mid-flight and remains present after the saccade lands. In this

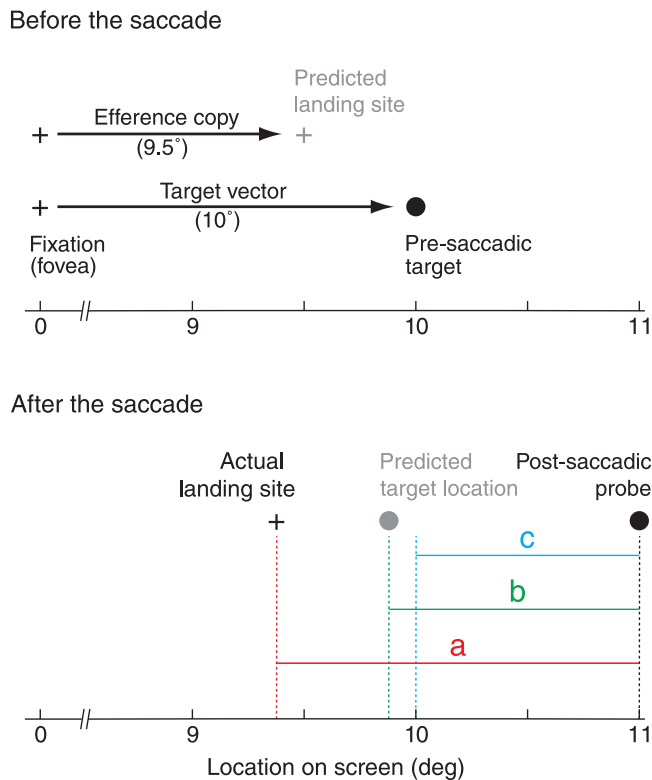


Figure 1. Perceived displacement from pre-saccadic target to post-saccadic probe. Following the presentation of the saccade target, the efference copy vector can be used to remap the target to its expected location following the saccade. In this example, the planned saccade is too short to land exactly on the target and the predicted target location is therefore about 0.5° to the right of the fovea. After the saccade, either this remapped location or the actual landing site could serve as a proxy for the pre-saccadic target location. If the perceived judgments of displacement to the post-saccadic probe are based on the actual saccade landing site, the distance *a* should correlate strongly with displacement judgments. Alternatively, the perceived displacement may be based on the remapped target location. If the efference copy used for remapping is reasonably accurate, the unpredicted error in landing will be small (about -0.125° in the example here), and the physical target offset *b* will be a fair estimate of the actual displacement *c*. In this case, the physical offset *b* should correlate strongly with displacement judgments.

case, small offsets of the saccade target during the saccade go undetected (Bridgeman, Hendry, & Stark, 1975; Deubel, Schneider, & Bridgeman, 1996). This saccadic suppression of displacement occurs right at the focus of attention, i.e. the saccade target location (Deubel & Schneider, 1996), as opposed to change blindness where only unattended modifications of the visual scene go unnoticed during a saccade (or during other transients, O'Regan, Rensink, & Clark, 1999). The displacement that is not seen is not lost, however, but treated as an oculomotor error (McLaughlin, 1967). In particular, if it

is repeated—a target at a given eccentricity is displaced by the same amount during the saccade on every trial—the saccade length itself will be adjusted to correct this “error” so that the saccade will land close to the displaced target. This phenomenon is known as saccadic adaptation (see Hopp & Fuchs, 2004, for a review) and can be evoked in healthy humans within a few minutes (50–100 trials).

Saccadic suppression of displacement has been used to argue that the remembered location of the pre-saccadic target, although available to the oculomotor system, is lost to perception. However, Deubel et al. (1996) showed that it is not (see also Deubel, 2004). They introduced a 250-ms blank between saccade onset and the appearance of the post-saccadic target and found that even very small displacements between the pre- and post-saccadic locations were accurately detected. In the classic saccadic suppression of displacement, a stimulus present immediately after the saccade in the vicinity of the expected target location is taken to be the target (Deubel, Bridgeman, & Schneider, 1998). Since the saccade eliminates the transient that would normally accompany a target displacement, the discrepancy between the new location of target and its expected location is attributed to oculomotor error (that can drive adaptation) rather than to object motion. However, if the target is not present upon saccade landing, it cannot override any representation of pre-saccadic location. The onset transient for this delayed new position appears to trigger an interpretation of the pre- and post-saccadic mismatch as object motion rather than saccade error.

How does the visual system recover the location of the original pre-saccadic target once the saccade has landed? This recovered location can be measured experimentally by the perceptual null location of the displacement judgments for the new, post-saccadic target relative to the pre-saccadic location (i.e. the location for which the pre- and post-saccadic locations are judged to be matching). Above we outlined several alternatives that could serve as a proxy for the pre-saccadic location of the target: the remapped target location, the saccade landing site, and the post-saccadic target location. The landing site of the saccade might serve as the proxy for the pre-saccadic location, as the saccade, after all, had been aimed to land on the target. However, Deubel et al. (1996) claimed that perceived displacement did not depend on the saccade landing site, reporting that displacement judgments were more accurately predicted by the physical post-saccadic target locations than by saccade endpoints. If the pre-saccadic location is recovered independently of individual saccade landing sites, it suggests that at least part of the oculomotor error of each saccade is known and can be used to recover the original target location. Specifically, the subtraction between the target vector and the efference copy vector may provide the necessary information about where the target should be relative to the saccade landing

site, as illustrated in [Figure 1](#). If the pre-saccadic target is at 10° and the efference copy vector for the saccade currently being programmed is 9.5° , then the oculomotor system is predicting an upcoming saccade that is slightly too short. Subtracting the efference copy vector from the target vector remaps the target to its predicted post-saccadic location (0.5° to the right of the landing site). The actual saccade may also deviate from the programmed landing due to unpredictable oculomotor error but if this unpredicted error is small relative to the predicted targeting error (difference between the target vector and the efference copy vector) then trial-to-trial variability in landing will be mostly accounted for by variability in the efference copy. In this case, perceptual judgments of displacement based on the remapped target location will be relatively independent of actual landing sites. However, another study suggested that discrimination of pre- to post-saccadic target displacement does depend on the saccade landing site (Bahcall & Kowler, 1999). In this study, saccadic adaptation was used to change the landing sites, and a post-saccadic blank interval was again used. As in Deubel et al.'s (1996) experiments, the blank served to avoid saccadic suppression of displacement and its consequence of taking the new target location, wherever it was, as a proxy for the pre-saccadic target location. Before adaptation, localization performance was veridical, but after adaptation the probe had to be shifted in the direction of adaptation to be perceived as aligned with the pre-saccadic target. The direction of the adaptive localization shift was correlated with the direction of adaptation in gain-increasing and gain-decreasing adaptation sessions.

The present study was interested in the factors that determine displacement judgments between pre and post-saccadic targets. We examined the effect of trial-to-trial variability in landing sites for saccades before and after adaptation and the effect of the mean shift of landing sites introduced by saccadic adaptation itself. If displacement discrimination is accurate, and not influenced by the trial-to-trial saccadic landing location (strengthening Deubel et al., 1996), information about the expected targeting error of individual saccades must be available, providing a remapped target as the proxy for the pre-saccadic target location. Following the adaptation session used in our experiment, saccades will land short of the target. If displacement judgments still have a null point at or near the original pre-saccadic target location, it would suggest that adaptation also affects the efference copy vector so that the remapped target would be accurately recovered despite adaptation. If, on the contrary, perceptual judgments are influenced by adaptation, the null point for displacement judgments will shift in the adapted direction. This would suggest either that the remapped target site is computed from an unadapted efference copy vector or that the localization of the pre-saccadic target itself is modified by adaptation (Awater, Burr, Lappe, Morrone, & Goldberg, 2005).

Methods

Participants

Nine volunteers from the Paris Descartes University community took part in the experiment (aged 29 ± 2 years; 4 women; 2 authors). All had normal or corrected-to-normal vision and gave their informed consent. The experiments were carried out according to the ethical standards laid down in the Declaration of Helsinki.

Instruments and stimuli

Participants were seated in a silent and dimly lit room with the head positioned on a chin rest, 63 cm in front of a computer screen. Stimuli were red (3.5 cd/m^2) and black (0.15 cd/m^2) 0.2° -diameter dots on a gray background (16.5 cd/m^2), presented on a 22" Formac ProNitron 22800 screen with a spatial resolution of 1024 by 768 pixels (or 36.7° by 27.6°) and a vertical refresh rate of 145 Hz. When a response was required, a short 45 ms fading pure tone was played. Movements of the right eye were measured using an EyeLink 1000 Desktop Mount (SR Research, Osgoode, Ontario, Canada) with an average spatial resolution of 0.25° to 0.5° , sampling at 1 kHz. The experiment was controlled by an Apple Dual Intel-Core Xeon computer; manual responses were recorded via a standard keyboard. The experimental software controlling stimulus display and response collection was implemented in MATLAB (MathWorks, Natick, Massachusetts, USA), using the Psychophysics (Brainard, 1997; Pelli, 1997) and EyeLink (Cornelissen, Peters, & Palmer, 2002) toolboxes.

Procedure

Participants were instructed to fixate a small red circular target that could appear at one of nine equiprobable locations ([Figure 2a](#)). Once fixation had been detected for more than 200 ms, the target turned black and, after a random delay of 500–1000 ms, jumped to a new location 10° to the left or right. Participants were instructed to follow the target with a saccade. In the test trials, saccade detection caused the target to disappear and the screen to remain blank for 250 ms. After this delay, the target reappeared at one of 13 equiprobable locations, from -3° to $+3^\circ$ to the left or right of the pre-saccadic location. Four hundred ms later a tone indicated that participants were to report the location of the post-saccadic target relative to the pre-saccadic target: left or right. In the adaptation trials, saccade detection caused the target to step from 10° to 8° (without a blank) and no response was required. These trial procedures are illustrated in [Figure 1b](#).

Saccade detection was implemented online by a boundary technique. When the recorded eye position left the

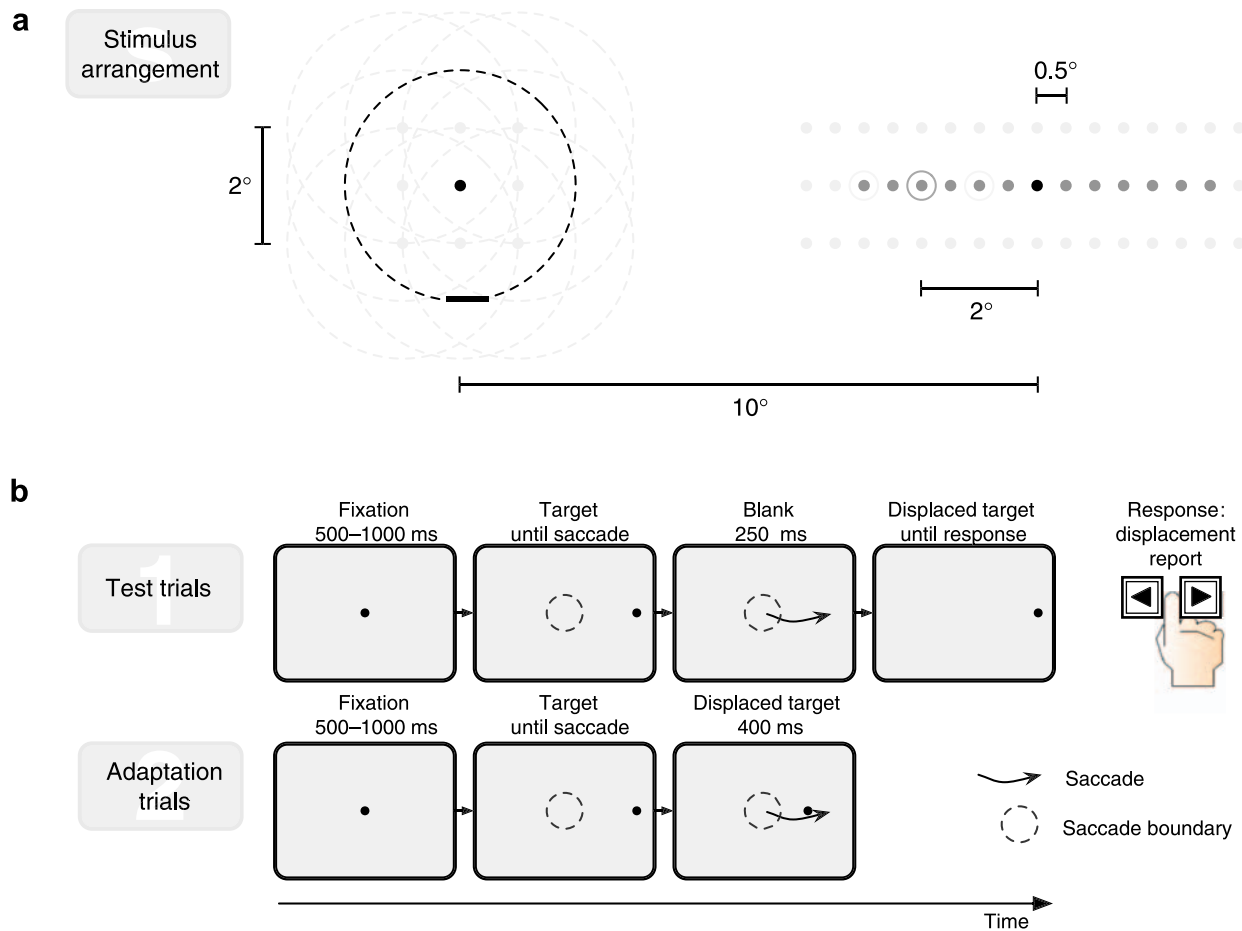


Figure 2. Spatial layout of the visual stimuli and trial procedure. (a) The fixation point could appear at one of the nine left-hand locations (center of the screen $\pm 1^\circ$ in x and y). For illustrative purposes, the central fixation is used as an example (dark colors); information for all other positions is presented in light gray. The target was always 10° away, on the same horizontal plane, here to the right. The target was removed when the eyes crossed a circular boundary with a diameter of 2° (dashed circles). The post-saccadic test locations in test trials included the pre-saccadic position as well as 6 to the left and 6 to the right in steps of 0.5° (dark-gray). During adaptation trials, during the saccade the target was displaced by -2° , highlighted by a small gray circle. (b) Observers fixated for 500 to 1000 ms before the fixation dot was displaced to a peripheral target location. A saccade to this location triggered the offset of the stimulus. In test trials (1), the stimulus reappeared 250 ms later at one of 13 test locations and a tone instructed observers to report the direction of displacement. In adaptation trials (2), the stimulus was displaced during the saccade and no report was required.

area within a 2° -diameter circle centered on the fixation target (dotted lines in Figure 2), the gaze-contingent changes were introduced (i.e. blanking or displacing the target). If a saccade was detected before target presentation, a warning appeared on the screen asking participants to maintain fixation and the trial was immediately rerun.

The experiment was divided into three parts. Each participant was tested in only one target-side condition (left or right). In the pre-adaptation block (234 trials), there were nine possible fixation target positions and thirteen possible post-saccadic target locations (-3° to 3° in steps of 0.5°). Each post-saccadic target location was tested 18 times (twice for each fixation position). In the adaptation phase (108 trials), the same nine fixation target positions were run 12 times each. Finally, the post-

adaptation block (702 trials) combined test trials (33%) and adaptation trials (67%). The adaptation trials were included to ensure that adaptation was maintained throughout the post-adaptation block. Trial types were run in a random order.

Data analyses

Eye movement data was analyzed offline. Saccades were detected using an improved version of the algorithm proposed by Engbert (2006). This algorithm has the advantage that it takes both two-dimensional velocity as well as intra-subject and intra-trial variability into account. Specifically, velocities were smoothed over 5

subsequent eye position samples in a trial. Saccades were detected as outliers in two-dimensional velocity space, exceeding the median velocity by 5 standard deviations for at least 8 ms (eight subsequent samples). In addition, if the algorithm detected two saccade events separated by 5 ms or less, they were counted as a single saccade. This ensured that amplitude and landing site measures took into account all potential saccadic overshoots.

Response saccades were defined as the first saccade that brought the eye less than 8° away from the pre-saccadic target. Trials including blinks or saccades larger than 1° prior to the response saccade were discarded, as were trials where no response saccade was detected offline. On average, 97.4% of the trials were included in final data analysis. Results were pooled over saccade direction (left and right), and responses were renamed “forward” (the post-saccadic target reappeared further from fixation) and “backward” (the post-saccadic target reappeared closer to fixation). We compared saccade latency, amplitude and point of subjective equality, which corresponds to the perceptual “null location” (PNL) between pre- and post-

adaptation tests with Student *t*-tests. Only test trials (not adaptation trials) were included in these analyses.

Results

Mean saccade latency ($\pm 95\%$ confidence interval) decreased from 179 ± 12 ms in the pre-adaptation to 166 ± 11 ms in the post-adaptation phase, probably due to practice ($t_{[8]} = 4.4$, $p < .003$). Saccade amplitude was significantly reduced by $1.25 \pm 0.22^\circ$ from $9.57 \pm 0.26^\circ$ in the pre-adaptation to $8.32 \pm 0.18^\circ$ in the post-adaptation block ($t_{[8]} = 11.3$, $p < 0.001$). This corresponds to a gain change of $-13.0 \pm 2.1\%$ ($[\text{post-adaptation amplitude} - \text{pre-adaptation amplitude}] / \text{pre-adaptation amplitude}$) and a compensation of $62.5 \pm 10.9\%$ of the 2° backward step ($[\text{pre-adaptation amplitude} - \text{post-adaptation amplitude}] / [\text{target step}]$). Figure 3a presents the time course of adaptation for a typical participant. Figure 3b shows the average change of saccade amplitude for all participants.

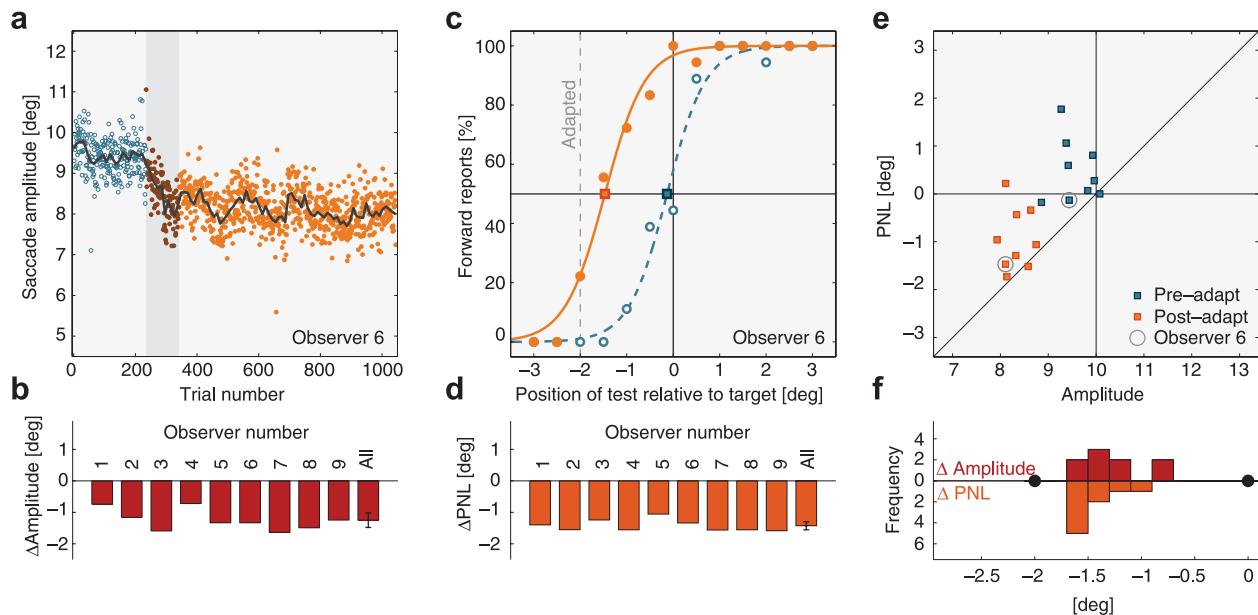


Figure 3. Saccade amplitudes and perceptual judgment of displacement. (a) Time course of adaptation (amplitude as a function of trial number) for an example observer. Each point is one saccade. The black curve is a moving average, computed using a Gaussian kernel. The differentially shaded areas highlight the pre-adaptation, adaptation, and post-adaptation phases. (b) Individual and average changes in mean saccade amplitude from the pre-adaptation to the post-adaptation phase. The error bar is a 95% confidence interval computed across subjects. (c) Percentage of “forward” reports for each test location, in pre-adaptation (open blue symbols) and post-adaptation (filled orange symbols) phases for an example observer. Psychometric functions were fitted to performance in the pre-adaptation (dashed blue line) and post-adaptation (solid orange line) phase (see text) to estimate the perceptual null location (amount of displacement leading to chance performance; highlighted by squares) for each individual. (d) Individual and average change in perceptual null location from the pre-adaptation to the post-adaptation phase. The error bar is a 95% confidence interval computed across subjects. (e) Correlation of saccade amplitude and perceptual null location within and across the pre-adaptation and post-adaptation phases. Each point corresponds to one participant. (f) Histograms of individual changes in saccade amplitudes (plotted upwards) and perceptual null locations (plotted downwards) from the pre-adaptation to the post-adaptation phases. Black dots highlight the positions in the graph that encode no change (right) and a full change (left). Changes in both variables were intermediate between these two extremes.

The perceptual null location (PNL) corresponds to the post-saccadic target location that resulted in 50% forward and 50% backward responses, i.e. the post-saccadic position that which was perceived as matching to the pre-saccadic target location. We determined each observer's PNL by fitting logistic psychometric functions to the perceptual report data in both pre- and post-adaptation phases. Figure 3c shows the results for one observer (same as in Figure 3a); Figure 3d shows all individual and the average PNL shifts. In the pre-adaptation block, the average PNL was $0.47 \pm 0.42^\circ$, revealing that post-saccadic targets that were at the same location as the pre-saccadic target were perceived as moving slightly backward, against the direction of the saccade, while to be perceived as stationary, targets had to be slightly forward-stepped, in the direction of the saccade. In the post-adaptation block, there was a shift of the psychometric function: the average post-adaptation PNL was $-0.95 \pm 0.42^\circ$, which was significantly less than 0 and significantly different from the pre-adaptation PNL ($t_{[8]} = 23.3$, $p < .001$). To be perceived as stationary, targets had to be stepped backward, and post-saccadic targets that had the same location as the pre-saccadic target were perceived as stepping forward. The change in PNL (Δ PNL) was on average $1.43 \pm 0.12^\circ$. These results are summarized in Figure 3e, where we plotted PNLs as a function of mean saccade amplitudes in the pre- and post-adaptation phases. There was no correlation between mean saccade amplitude and PNL in the pre-adaptation ($R^2 = 0.02$, $p = 0.73$)

or post-adaptation phases ($R^2 = 0.00$, $p = 0.97$), nor between the amount of adaptation and the Δ PNL ($R^2 = 0.03$, $p = 0.66$). This might be due to the rather small range in which these effects would have to unfold. This can be seen in Figure 3f, which shows histograms of Δ PNL and Δ Amplitude for our nine subjects. This graph also highlights that the adaptation-related changes in mean saccade amplitude and PNL were intermediate between no change and a full 2 degree change in all individuals tested.

The shift of PNL following adaptation replicates earlier findings (Bahcall & Kowler, 1999) and suggests that perceptual judgments of location after saccadic adaptation do not take the actual saccade amplitude into account, resulting in an illusory displacement of blanked targets when they reappear at the same location after an adapted saccade. In a next step, we examined whether post-saccadic localization also varied as a function of eye position relative to the post-saccadic target. As suggested by the perceptual changes after saccadic adaptation, the actual eye position could be the anchor for perception, and other post-saccadic objects may be realigned around this position. This would be similar to the “landmark” effect (Deubel, 2004) in which a displaced target is seen as stationary when it is immediately present after the saccade, and nearby objects which are blanked but remain stable are seen to be moving.

Figure 4a presents performance as a function of landing site relative to the pre-saccadic target. Individual eye-position data was quantized independently for the pre- and post-adaptation phases. Means and confidence inter-

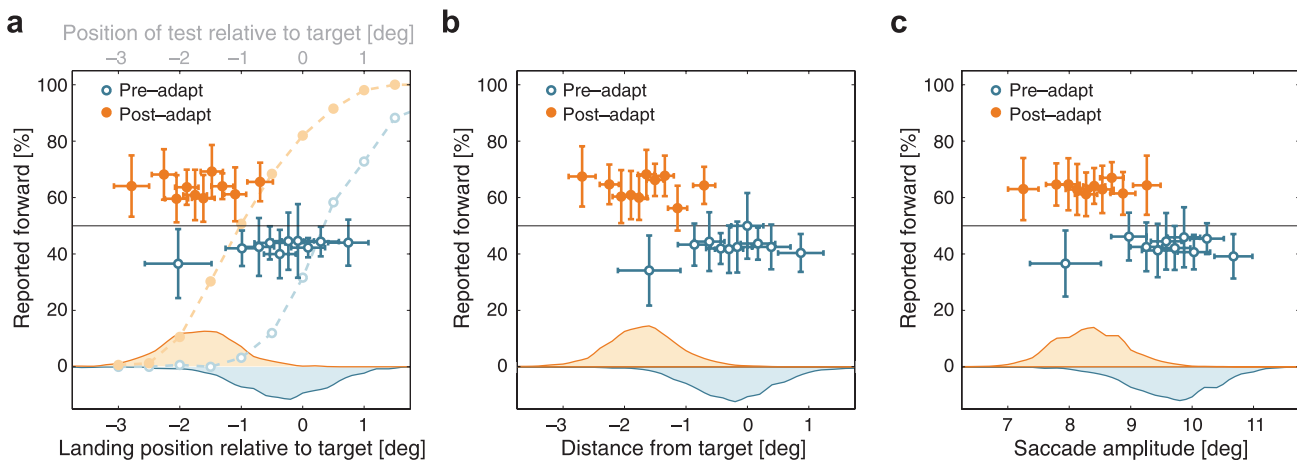


Figure 4. Relation between saccade landing site and post-saccadic location judgment. Mean percentage of “forward” reports in pre-adaptation (open blue symbols) and post-adaptation (filled orange symbols) phases is shown as a function of three different descriptions of the eye position following the saccade: (a) landing site (saccadic landing site relative to pre-saccadic target). (b) distance of eye position from the pre-saccadic target when test stimulus is presented (mean horizontal position in the first 50 ms after the appearance of the displaced target, approximately 100 ms on average after saccade landing), and (c) saccade amplitude (distance between starting and landing site of saccade). For each observer, deciles of these variables were determined and the percentage of forward reports was computed for trials corresponding to these deciles. Means across subjects are shown with 95% confidence intervals. Histograms at the bottom illustrate pooled distributions of each position variable for pre-adaptation (plotted downwards) and post-adaptation phase (plotted upwards). For comparison, the dashed curves in the background of panel a show the response data as a function of the position of the *test stimulus* (as opposed to the eye position, blue for pre-adaptation and orange for post-adapt, curves from Figure 2) with axis labeled on top.

vals of percent forward responses were computed for each decile. The figure shows a flat function, revealing that perceived displacement did not depend on the landing site of the eye. For comparison, we also plotted the same data averaged across subjects as a function of test location relative to the target (dotted lines in the background of Figure 4a). Clearly, there is no influence of trial-by-trial eye-position variability, neither in the pre-adaptation nor in the post-adaptation phase, although the range of eye positions was comparable to the range of displacements used. The same results were obtained when we computed the function for deciles pooled all subjects' data (data not shown). In addition, we computed point-biserial correlations between landing site and perceived displacement. For only one of nine subjects and only in the pre-adaptation phase, we observed a significant, but very small correlation ($R^2 < 0.03$, $p = .001$). For all other subjects there were no significant correlations in either phase (all individual $R^2 < 0.02$, all p values $>.078$). One might argue that the eyes' landing site is not the critical measure, as eye position can change slightly after the saccade. However, the same pattern of results was obtained if instead of landing site, eye position at target appearance (mean horizontal eye position in the first 50 ms after target reappearance, i.e., about 100 ms after the initial saccade; Figure 4b) or saccade amplitude (Figure 4c) were used as dependent variables (all $R^2 < 0.04$, all p values $>.058$ except the same subject as before, $p < .016$). On average, these eye position variables each accounted for less than 1% of the variance in the perceptual-report data.

Discussion

Discrimination of the direction of displacement informs about how we process information about egocentric spatial location. Our results allow us to examine the contribution of different factors to displacement direction discrimination: the remapped target location, the saccade landing site and the post-saccadic target location. Our results show that oculomotor variability does not influence judgments about displacement direction, which are based on veridical displacement size rather than on the retinal distance between actual saccade landing site and the reappeared target. Therefore, it appears that neither the landing site nor the post-saccadic target location serves as a proxy for the pre-saccadic location. The post-saccadic target was not taken to be at the pre-saccadic location presumably because the blank avoided saccadic suppression of displacement. On the contrary, discrepancies between the pre- and post-saccadic target locations were accurately detected—except for the effect of adaptation. Indeed, the adaptive modification of the saccade landing site introduced a systematic bias in displacement direction judgments: displacement discrimination shifted in the direction opposite to adaptation and stationary targets

were seen as moving forward while backward displaced targets were seen as stationary.

Our results are similar to those found by Bahcall and Kowler (1999). In their study, after adaptation, a blanked post-saccadic probe had to be shifted in the direction opposite to adaptation to be perceived as aligned with the pre-saccadic target—just as in the present results. These authors did not obtain a full psychometric function, and did not examine the correlation between actual saccade landing site and perceptual reports within a session, as we did here, however the direction of the perceptual shift was correlated with the direction of adaptation in gain-increasing and gain-decreasing adaptation sessions. While we did not find a correlation between the amount of backward adaptation and the extent of the perceptual shift, the correlation in the Bahcall and Kowler (1999) data seems to arise primarily from the difference between gain-increasing and gain-decreasing sessions.

We propose that a prediction about the post-saccadic retinal coordinates of the pre-saccadic target, i.e., remapping, is generated based on an efference copy that accurately represents the metrics of the upcoming saccade. This prediction would subsequently be compared to the actual post-saccadic retinal coordinates, and deviations attributed to object displacement. However, the absence of a correlation between displacement discrimination and landing site in the present data suggests that the prediction would include information about oculomotor variability, allowing small, normal deviations of saccade landing position to be discounted (i.e. not to be attributed to object motion). Including such information about oculomotor variability means that the system can predict that a post-saccadic target will be non-foveal.

However, the change of PNL with adaptation suggests that the actual eye movement does play a role in displacement discrimination. Based on the remapping mechanism proposed above, there are two possible interpretations for the pattern of perceptual reports following saccadic adaptation.

First, the efference copy may not include information about adaptation. Therefore, any difference between the predicted or remapped target location and the actual post-saccadic target location due to the adaptive shift of saccade landing site would be interpreted as object motion in the outside world. For example, a pre-saccadic target at 10° would lead to an efference copy of $\sim 10^\circ$, and the expected location of a stationary target would be roughly foveal. Following the adapted saccade of, say, 8.5° , stationary targets would be seen as moving forward while backward-stepped targets would be seen as stationary. Indeed, if the predicted post-saccadic retinal location of a target does not change and if the efference copy vector itself is not adapted, then the predicted post-saccadic retinal target location will match the actual post-saccadic retinal target location when the target displacement is equal to the size of adaptation. In the absence of real displacement, the actual post-saccadic retinal target

location will be farther than the predicted post-saccadic retinal location (because of the backward adaptation), leading to reports of forward jumps for stationary targets. This interpretation supposes that the shift in PNL should be equal to the amount of adaptation. Our results suggest a shift slightly larger than the amount of adaptation, however this may simply reflect the fact that in our paradigm adaptation had not yet reached its asymptote. According to this hypothesis, the two components contributing to variability in saccade landing site (oculomotor variability and an adaptive shift), are not taken into account by perception in the same way: oculomotor variability would be discounted by perception, but saccadic adaptation would not, suggesting that adaptation is not increased (albeit non-random) oculomotor variability. Perception would have substantial but partial knowledge about the saccadic system, based on an efference copy carrying information about normal oculomotor variability but not adaptation.

A second interpretation of our results is that saccadic adaptation modifies the perceived location of the pre-saccadic target (as suggested by Awater et al., 2005; Bruno & Morrone, 2007; Collins, Doré-Mazars, & Lappe, 2007). If such perceptual mislocalizations occurred, pre-saccadic targets at 10° would be perceived at, say, 8.5° and a saccade of this amplitude prepared. Supposing the efference copy matches the saccade, this would lead to stationary reports for backward-stepped targets, and forward reports for stationary targets, i.e., the pattern of results observed. According to this hypothesis, efference copy would carry correct metric information about adapted saccades, based on a modified perceived target location. This interpretation has the merit of also explaining some other mislocalization data (Awater et al., 2005; Bruno & Morrone, 2007; Collins et al., 2007), which the previous interpretation cannot do. Awater et al. (2005) tested probe localization in the vicinity of the saccade target and observed local perceptual mislocalizations many hundreds of milliseconds before a saccade, suggesting that saccadic adaptation induced a remapping of visual space. Furthermore, Collins et al. (2007) showed—as in the present study—that these mislocalizations were not proportional to the amplitude of the performed saccade. Instead, they were proportional to the adaptation of the saccade to the probe, suggesting that adaptation induced a common modification of perception and action in a particular region of space. Finally, Bruno and Morrone (2007) found that both verbal and pointing reports of perceived location shifted with adaptation, suggesting again a similar recalibration of action and perceptual maps. These studies suggest that saccadic adaptation is accompanied by a local modification of perceived location of visual objects. Our results are compatible with this hypothesis. Furthermore, other studies have shown that adaptation is taken into account in motor tasks requiring efference copy. In particular, correctly programming a sequence of memory-guided saccades requires combining

visual information about the second saccade target, encoded before sequence onset, with an efference copy of the intervening first saccade (Sommer & Wurtz, 2004). When the first saccade was adapted, second saccades remained accurate and compensated for the adaptation, showing that the efference copy provided correct information about the adapted metrics of the first saccade (Doré-Mazars, Vergilino-Perez, Collins, Bohacova, & Beauvillain, 2006).

In summary, our results suggest that metric information about upcoming saccades, in the form of an efference copy signal, plays a crucial role in determining the localization of visual objects across saccades. Because saccades occur several times per second, trans-saccadic perception is not a special case but represents the normal mode of perception; perceptual localization based on efference copy signals would therefore be the basic mechanism by which visual objects are localized in space. Our results show that efference copy signals carry information about normal oculomotor variability, allowing trial-to-trial variability in saccade landing sites to be discounted by perception. Saccadic adaptation modifies saccade landing site and may also induce a local modification of the perceived location of visual objects. Efference copy would match the planned upcoming saccade, be it based on a veridically localized target or on a target whose localization is distorted by adaptation itself.

Acknowledgments

Thérèse Collins and Martin Rolfs contributed equally to this work. This research was supported by an Alexander von Humboldt Research Fellowship to Thérèse Collins and a Chaire d'Excellence grant to Patrick Cavanagh.

Commercial relationships: none.

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