Motor signals in visual localization

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We demonstrate a strong sensory-motor coupling in visual localization in which experimental modification of the control of saccadic eye movements leads to an associated change in the perceived location of objects. Amplitudes of saccades to peripheral targets were altered by saccadic adaptation, induced by an artificial step of the saccade target during the eye movement, which leads the oculomotor system to recalibrate saccade parameters. Increasing saccade amplitudes induced concurrent shifts in perceived location of visual objects. The magnitude of perceptual shift depended on the size and persistence of errors between intended and actual saccade amplitudes. This tight agreement between the change of eye movement control and the change of localization shows that perceptual space is shaped by motor knowledge rather than simply constructed from visual input.

Keywords: active vision, eye movements, plasticity, spatial cognition, spatial vision

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Introduction

When a saccadic eye movement is initiated to an eccentric target, the oculomotor needs to steer the eye to the target location without visual feedback since latencies in the visual system delay visual feedback about the accuracy of the eye movement until after the saccade is finished. Thus, if a saccade is inaccurate the error between the final gaze direction and the target can only be registered after the saccade. This post-saccadic visual error is used by the oculomotor system to check saccadic accuracy and, if needed, recalibrate motor control for subsequent saccades to be more accurate (Kommerell, Olivier, & Theopold, 1976). In the experimental paradigm of saccadic adaptation, a post-saccadic visual error is introduced artificially by stepping the target while the saccade is in flight (Mclaughlin, 1967). The oculomotor system registers the post-saccadic error and adapts saccade behavior accordingly (Noto & Robinson, 2001; Wallman & Fuchs, 1998). Over the course of several such trials, the amplitude of the saccade to the target eventually matches the stepped location of the target, rather than the initial location (Figure 1B). The saccadic adaptation procedure, therefore, introduces a dissociation between the physical location of the target as registered by the retina and the motor program that is executed to shift gaze onto that target. Saccade amplitudes can be lengthened or shortened depending on whether the saccade target is displaced in inward or in outward direction. Differences between inward and outward adaptations (Ethier, Zee, & Shadmehr, 2008; Hernandez, Levitan, Banks, & Schor, 2008; Panouilleres et al., 2008) and between different types of saccades (Alahyane et al., 2007; Collins & Dore-Mazars, 2006; Deubel, 1995; Erkelens & Hulleman, 1993; Fujita, Amagai, Minakawa, & Aoki, 2002; Hopp & Fuchs, 2004) suggest that multiple mechanisms of saccadic adaptation exist that operate at various stages of the oculomotor transformation.

Saccadic adaptation has profound influences on trans-saccadic visual perception. In trans-saccadic localization, the location of a visual stimulus that is briefly presented before a saccade has to be reported after the saccade is finished. After saccadic adaptation, the location report is shifted in the direction of the adaptation (Awater, Burr, Lappe, Morrone, & Goldberg, 2005; Bahcall & Kowler, 1999; Bruno & Morrone, 2007; Collins, Dore-Mazars, & Lappe, 2007). This shift in the perceived position is independent of other peri-saccadic mislocalization effects such as peri-saccadic compression (Georg & Lappe, 2009). Trans-saccadic perception may use an efference copy of the saccade motor command to remap the pre-saccadic position of an object to its predicted post-saccadic location (Melcher & Colby, 2008; Sperry, 1950; von Helmholtz, 1896; von Holst & Mittelstaedt, 1950). Trans-saccadic mislocalization would be expected if the efference copy signal does not match the executed saccade. For example, if the efference copy signal is not informed about the amplitude change induced by saccadic adaptation, and thus signals an unadapted saccade, all remapped locations would be uniformly shifted by the amount of the amplitude adaptation (Bahcall & Kowler, 1999). However,

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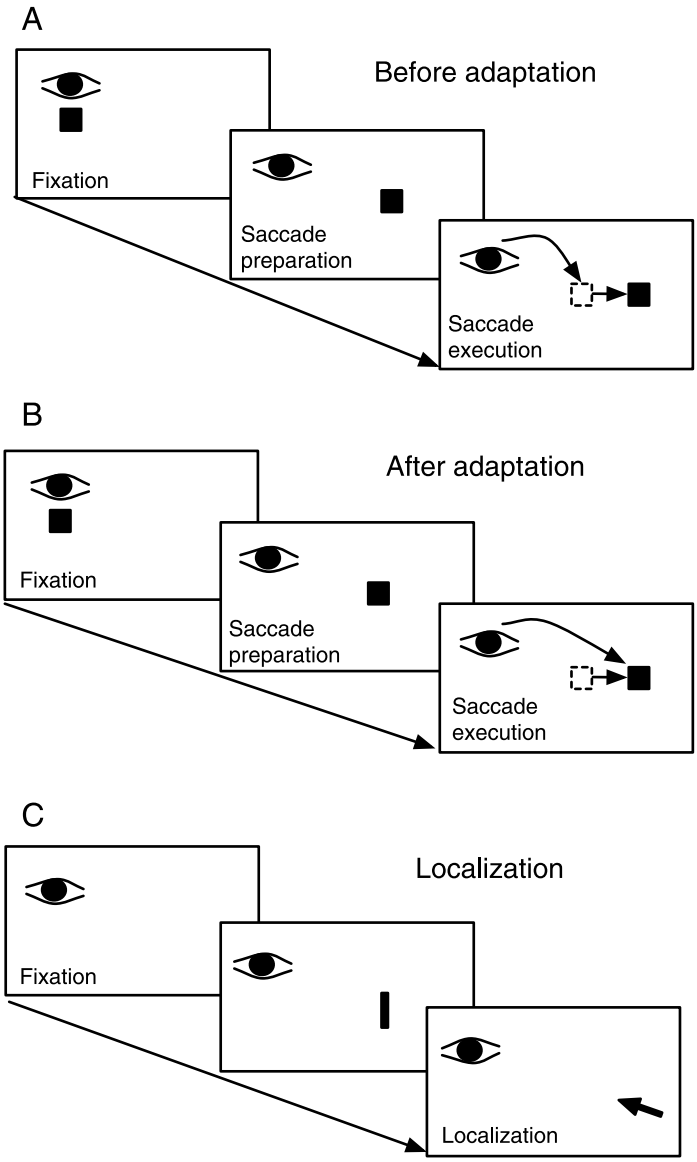

Figure 1. Saccadic adaptation and visual localization. (A) At the beginning of an adaptation session, the eye of the subject fixates a target on a black screen. When the target jumps 13 deg to the left, the subject prepares a saccade. Then, while the saccade is underway, the target is stepped further 3 deg to the right. At the time of arrival, the saccade has not reached the target, and a post-saccadic error is registered that corresponds to the distance of the target from the fovea after the saccade. (B) After several adaptation trials, the saccade amplitude increases, such that the eye now lands closer to the final target location. (C) Intermixed within the course of adaptation trials were localization trials. In these, the subject had to keep a constant eye position in darkness while a localization probe was briefly presented 13 deg in the visual periphery. The subject had to indicate the perceived location of the probe with a mouse pointer.

detailed analysis of the trial-by-trial covariance of saccade amplitude and perceptual localization shows that the efference copy signal is a faithful indicator of saccade amplitude variability even after saccadic adaptation (Collins, Rolfs, Deubel, & Cavanagh, 2009). Moreover, perceptual mislocalizations are not uniformly shifted throughout the visual field but occur only in the vicinity of the saccade target (Awater et al., 2005; Collins et al., 2007).

A different explanation for the adaptation-induced mislocalization is that visual localization is linked to saccade targeting, and that because saccadic adaptation modifies saccade target commands it also modifies visual localization (Awater et al., 2005; Collins et al., 2007; Zimmermann & Lappe, 2009). This explanation does not rely on the efference copy signal as a means for trans-saccadic visual localization but suggests that adaptation takes place in brain structures that support both visual localization and saccade targeting. If saccade motor vectors are indeed used for visual localization, adaptation-induced mislocalization should also be observable during fixation when no saccade is executed. To test this, we combined a series of adaptation trials with an interspersed localization task in which subjects had to indicate the apparent position of a visual stimulus but were not allowed to perform any saccade. Thus, unlike earlier studies that had shown a shift of perceived location after the execution of an adapted saccade our study tested whether the adapted state itself is associated with a shift of perceptual localization, even when no saccade is performed. This procedure has the advantage of testing distortions in visual localization directly without any confounding influence of trans-saccadic position memory.

Methods

Setup

The subject sat in a completely dark room in front of a computer monitor, which displayed target and localization stimuli. Care was taken to avoid any visual stimulation other than that displayed on the monitor. This was done to prevent the use of landmarks or references for localization (Awater & Lappe, 2006; Deubel, Schneider, & Bridgeman, 2002). The subject was seated 57 cm in front of a 22″ computer screen (Eizo FlexScan F930) with the head stabilized by a chin rest. The visible screen diagonal was 20″, resulting in a visual field of 40 deg × 30 deg. Stimuli were presented on the screen with a vertical frequency of 120 Hz at a resolution of 800 × 600 pixels. The room was completely dark. To avoid visibility of the screen borders, the display was covered with a transparent foil that reduced the luminance by about 2 log units. Eye movements were monitored by the Eyelink 1000 system (SR Research, Canada), which samples gaze positions with a

frequency of 1000 Hz. Viewing was binocular but only the dominant eye was recorded.

Saccade trials

At trial onset, a fixation point (0.75 × 0.75 deg) appeared at a horizontal position 10 deg to the left of the central position. The vertical position varied from trial to trial and was a randomly assigned value between 10 deg above and 10 deg below the screen center. This method is preventing fatigue effects due to a monotonous setup. The subject was instructed to direct gaze on the fixation point. The fixation point was presented for 800 ms plus a randomly chosen period between 0 and 300 ms. Simultaneous with the offset of the fixation point a saccade target (0.75 × 0.75 deg) appeared 13 deg to the right of the fixation point. The subject performed a saccade to the target as soon as possible. The trial ended 830 ms after saccade target onset. A saccade trial lasted therefore between 1630 and 1930 ms. The next trial started automatically.

Saccadic adaptation

Saccadic adaptation was induced with two different methods. In the standard saccadic adaptation method (Mclaughlin, 1967), the saccade target was displaced by a fixed distance of 3 deg as soon as the eye tracker detected the gaze position to be more than 2.5 deg rightward of the fixation point. Inward adaptation was induced by a target displacement to the left. Outward adaptation was induced by a target displacement to the right.

The second adaptation method used a target displacement that was yoked to the end point of the eye movement (Robinson, Noto, & Bevans, 2003). The saccade landing position was predicted online, and the saccade target was displaced to a location with a constant distance to the predicted landing position of the saccade. The prediction of the saccade landing position used a velocity criterion to determine the end of the saccade. Gaze position was sampled with 1000 Hz and saccade velocity was calculated online by dividing the mean distance the eye traveled within three successive samples by the mean duration of the three samples. When the velocity sank below 30 deg/s, the current gaze position was taken as the prediction of the saccade landing point. Target displacement was calculated from this position. The landing point prediction was very accurate with a mean error of 0.1 deg (*SE* 0.16 deg).

The eye movement registration and the update of the computer screen for the target displacement took about 12 ms. Therefore, target displacement took place slightly after the end of the saccade. This is not critical for the induction of adaptation, however, since saccadic adaptation can be induced with target displacements that take place up to 80 ms after saccade end (Fujita et al., 2002).

Six different constant visual errors were applied in separate sessions: −1, −2, and −3 deg for inward adaptation and 1, 2, and 3 deg for outward adaptation.

Localization trials

Localization was tested in a block of trials before adaptation (baseline) and in 5 blocks of trials interleaved in the course of adaptation. Each block contained 20 localization trials. Subjects were instructed to direct gaze at the center of the screen and avoid any eye movement during the entire block of localization trials. A fixation point was not provided, in order to avoid that it may be used as a visual landmark for localization. Rather, the eye tracker sampled gaze position online to check the gaze stability of the subject.

When ready, the subject pressed the space button on the keyboard to start a trial. Thirty milliseconds later, a small bar (0.2 × 3 deg, 0.02 cd/m^2, white) appeared 13 deg to the right of the subject's current gaze position. The bar was flashed for 30 ms. One thousand milliseconds after bar offset, a mouse pointer appeared on the right border of the screen. The mouse pointer appeared at the bottom border of the screen and a randomly chosen horizontal position between 35 deg and 40 deg with respect to the left side of the monitor. The subject moved the mouse pointer to the perceived position of the bar and pressed the mouse button. Gaze fixation was continuously monitored throughout this procedure. After the mouse button was pressed, the mouse pointer disappeared and the subject could start the next trial with the space button. A localization trial lasted 2–3 s. The localization error was calculated as the deviation of the mouse click position from the position where the bar was presented. Trials in which the subject broke fixation or failed to see the bar were discarded. This occurred in 12% of all localization trials.

Trial sequence

After every 200 adaptation trials, localization was tested in a block of 20 trials (Figure 1C). A similar block of 20 localization trials at the beginning of the experiment served as a baseline of localization performance before saccadic adaptation. Likewise, an initial block of 40 saccade trials without the adaptation step of the target served as a baseline for saccade performance.

Mimic saccades

To analyze, whether saccade adaptation induced changes in peak velocities, sessions were run, which

allowed to compare peak velocities of adapted saccades with peak velocities of unadapted saccades with the same amplitude size. Since saccade velocities depend on saccade amplitudes, we chose saccade amplitudes from the adaptation sessions and used them to determine saccade target position in the mimic trials. For each adaptation session, a mimic saccade session was run, which included the same number of trials and was intended to elicit the same saccade amplitudes. In each trial of the mimic saccade session, the saccade target was placed at the saccade end point of the corresponding trial of the adaptation session and stayed there throughout the saccade. We then compared saccade characteristics from the adaptation trials with the mimic trials. In the analysis, we compared saccade amplitudes of trial n from the adaptation session with saccade amplitude of trial n from the mimic adaptation session. We analyzed all trials in which saccade amplitudes in the adaptation condition did not differ more than 0.5 deg from the mimic condition. The comparison was accomplished for standard adaptation data and constant error adaptation data.

Participants

Five subjects (4 females, 1 male, mean age: 25) participated in the inward adaptation experiments. Five different subjects (4 females, 1 male, mean age: 28) participated in the outward adaptation experiments. The order of all adaptation sessions was counterbalanced across subjects. For every subject, a break of at least 48 h was interposed between successive sessions. For outward adaptation with a 3 deg constant visual error, only 4 subjects were measured in the mimic adaptation condition. In this condition, only data from 4 subjects were compared.

Results

Standard adaptation method

Modifications of saccadic amplitudes with the standard saccadic adaptation had a clear effect on visual localization (Figure 2). While saccade amplitude (gray dots) changed from 12.5 deg (*SD* 2.14 deg) in the pre-adaptation baseline trials to 13.8 deg (*SD* 1.01 deg) at the end of the adaptation period, perceived location (black dots) changed from 12.0 deg (*SD* 0.59 deg) to 14.0 deg (*SD* 0.84 deg). To compare saccade amplitude changes and localization changes over the course of adaptation, we calculated the deviation of each localization block from the pre-adaptation baseline trials. The localization change was calculated as the difference between median localization in the baseline trials and median localization in each of the 5 localization blocks during adaptation. The amplitude change was calculated as the difference between median saccade amplitudes in the baseline trials and median saccade amplitudes around the time when localization was tested, i.e., the last ten trials before a localization phase and the following ten trials after that localization phase. Figure 3A shows the amount of adaptation (dashed line) and the amount of mislocalization (solid line) averaged over 5 subjects. Adaptation reached a maximal amplitude increase of 1.4 deg (*SE* 0.23 deg), or 46% of the 3 deg outward target displacement. Localization developed very similarly to the adaptation and also changed over the course of trials (repeated measures ANOVA, $F = 7.425$, $p = 0.016$). After 1000 trials of adaptation localization probes were mislocalized by 1.5 deg (*SE* 0.31 deg) in the direction of adaptation.

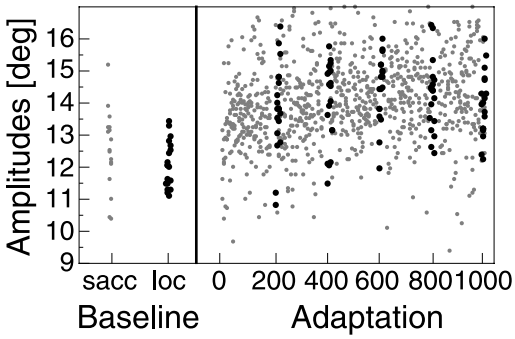

Figure 2. Development of saccadic adaptation and localization changes over the course of a single adaptation session. In baseline trials without adaptation steps of the target, saccade amplitudes (gray points) and probe localizations (black points) lie around 12.5 deg and 12 deg, respectively. During the course of adaptation, saccade amplitudes increased to 13.8 deg. Location judgments changed along with the adaptation resulting in an average mislocalization of 2 deg for this subject.

These results clearly show that modifications of saccadic amplitude by saccadic adaptation are paralleled by associated changes in visual localization. This is consistent with our hypothesis that oculomotor knowledge is used for perceptual space, and cannot be explained by mismatches between eye movement and efference copy signals (Bahcall & Kowler, 1999) because the localization task was performed during steady fixation. However, a different pattern of results appeared when the saccadic adaptation was induced in the opposite direction, i.e., by an intra-saccadic step of the target to the left, which induces a shortening of saccade amplitude (Figure 3B). This experiment was done with the same methods as before with the only exception that the target stepped 3 deg to the left during the initial saccade. The inward step of the target induced a strong adaptation of saccade amplitude (-2.2 deg (*SE* 0.26 deg), or 73% of the target displacement) but no localization change.

This difference between inward and outward saccadic adaptations may be related to partially different mecha-

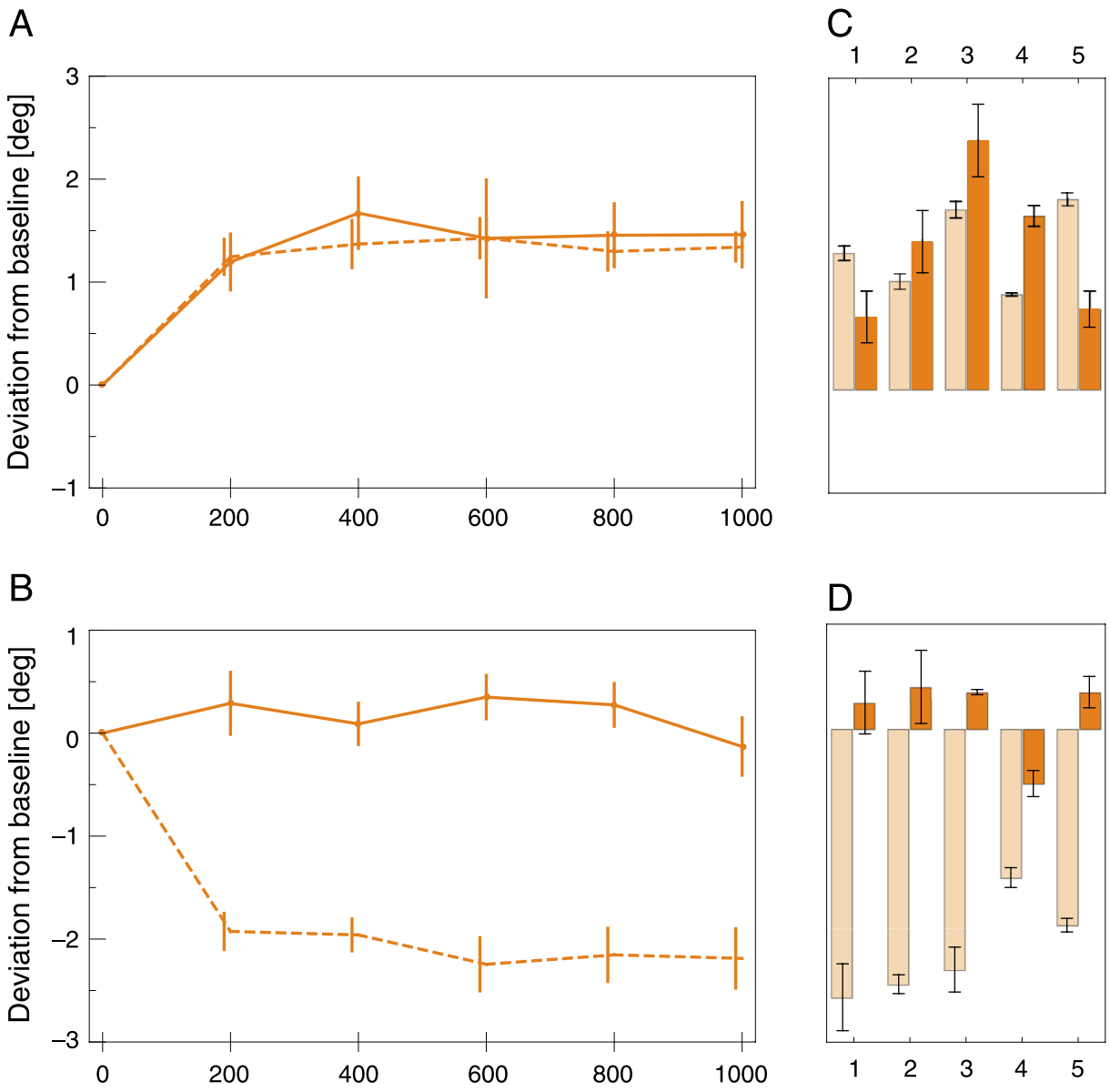

Figure 3. (A, B) Mean mislocalization (solid line) and mean adaptation (dashed line) averaged over all subjects. Error bars are standard errors. (A) Outward adaptation and (B) inward adaptation sessions. (C, D) Mean mislocalization (dark orange) and mean adaptation (light orange) averaged within each subject. Error bars are standard deviations. (C) Outward adaptation and (D) inward adaptation sessions.

nisms for the two directions of adaptation (Ethier et al., 2008; Golla et al., 2008; Panouilleres et al., 2008). Inward adaptation is faster and stronger than outward adaptation (Bahcall & Kowler, 1999; Noto, Watanabe, & Fuchs, 1999; Robinson, Noto, & Bevans, 2003) and can be achieved by decreasing saccade velocity and taking advantage of the system's tendency to fatigue (Golla et al., 2008). Decreasing saccade velocity is an energetically efficient way to achieve smaller saccade amplitudes (Ethier et al., 2008). Outward adaptation, on the other hand, inevitably requires more effort to sustain, and energy considerations suggest that it would best be achieved by changing the saccade target signal (i.e., remap the target location) rather than manipulate saccade dynamics (Ethier et al., 2008). This difference may explain why inward adaptation is less tied to localization: it relies on a lower level mechanism of adaptation. In order to estimate whether adaptation was based on a remapping of the target signal or on a change in the dynamic control of the saccade, we compared velocity profiles from the adapted saccades and from separate sessions of 1000 saccade trials without adaptation, but in which the saccade amplitude was the same as in the adaptation session (Ethier et al., 2008). These mimic adaptation sessions were designed to evoke the same amplitude sizes in the same trial order as in the adaptation sessions and thus allow a direct comparison of the mean peak velocities. Mean peak velocity in inward adaptation sessions was 357 deg/s (*SE* 10 deg/s), significantly lower than that of the mimic sessions (390.8 deg/s (*SE* 16.61 deg/s), one-tailed paired *t*-test, $p = 0.014$).

Mean peak velocity in outward adaptation sessions was 475 deg/s (*SE* 5.83 deg/s) and not significantly different from that of the mimic sessions (477 deg/s (*SE* 26.04 deg/s), one-tailed paired *t*-test, $p = 0.237$). Figure 4 shows peak velocity data in the two conditions separately for each of the five subjects. This analysis confirmed different mechanisms for inward and outward adaptations and further suggested that only the mechanism of target remapping during outward adaptation provides a link to visual localization.

Constant error adaptation method

We next wondered whether it would be possible to induce target remapping also for inward adaptation. Since the modification of the saccade dynamics that underlies inward adaptation is a faster process than the modification of the target command (Chen-Harris, Joiner, Ethier, Zee, & Shadmehr, 2008), inward adaptation asymptotes rather quickly to a stable state in which the post-saccadic error is small. We reasoned that, if the post-saccadic error would remain high for a longer number of trials, then target remapping may become relevant also during inward adaptation. We tested this prediction in a paradigm that creates a constant post-saccadic error (Robinson, Noto, & Bevans, 2003). In this paradigm, the saccade landing position is predicted from in-flight measurements of gaze position and the target is stepped to a location that is a constant, pre-determined distance from the predicted landing position of the saccade. Thus, the saccade can never reach the target, and, independent of how accurate or how adapted the saccade to the initial target is, there is always a post-saccadic error that continuously steers saccadic adaptation toward lower amplitudes. We used this procedure with three different error sizes (−1, −2, and −3 deg) for inward adaptation, and, for comparison, also with three sizes (1, 2, and 3 deg) for outward adaptation. Each constant visual error condition was tested in a separate session.

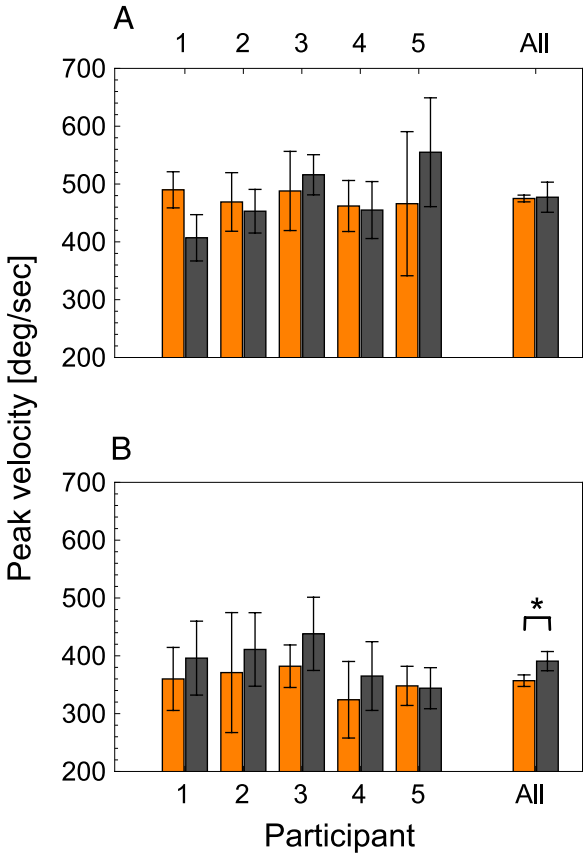

Figure 4. Mean peak velocities in the adaptation (orange) and the mimic (gray) conditions averaged within each subject and over all subjects. Error bars are standard deviations. (A) Outward adaptation and (B) inward adaptation sessions.

The amount of adaptation that we obtained with this procedure increased with post-saccadic error size for both adaptation directions (Figures 5A and 5C). After 1000 trials, every constant post-saccadic error condition produced a stronger adaptation than the normal method (gray curves in Figures 5A and 5C). Moreover, for large constant errors adaptation continues to increase over the entire duration of the experiment, showing that the adaptation mechanism asymptotes very slowly.

The constant post-saccadic error method succeeded in inducing localization changes for inward adaptation when the post-saccadic error was large (Figure 5D). For adaptation with a 3 deg constant error, the maximal mislocalization of −1.41 deg (*SE* 0.37 deg) was reached after 600 trials (ANOVA, $F = 2.079$, $p = 0.019$). Mislocalization after inward adaptation with 1 deg and 2 deg was not different from zero. Increasing amounts of mislocalization that are observable after 1000 trials (−0.24 deg (*SE* 0.3 deg) for 1 deg constant visual error and −0.68 deg (*SE* 0.46) for 2 deg constant visual error) are due to the results from one subject only.

Figure 5C shows that adaptation magnitude grew with increasing visual error size. Adaptation with constant post-saccadic errors induced stronger adaptation than the normal method. To decide whether mislocalization depends on the amount of saccade adaptation or rather on the size of the post-saccadic visual error, we included an additional condition. With the normal adaptation method, we applied a 5 deg target displacement in inward direction. In this condition, adaptation was quickly achieved with a maximal mean value of −4.52 deg (*SE* 0.41 deg). Since mislocalization was completely absent, 0.13 deg (*SE* 0.35 deg) changes in visual localization depend on large and permanent post-saccadic errors. For outward adaptation (Figure 5B), localization changes for 2 deg and 3 deg constant post-saccadic errors were significant (repeated measures ANOVA, $F = 13.203$, $p = 0.001$ at 2 deg; $F = 5.501$, $p = 0.023$ at 3 deg) and identical to those of the normal method. The constant post-saccadic error of 1 deg induced virtually no localization change.

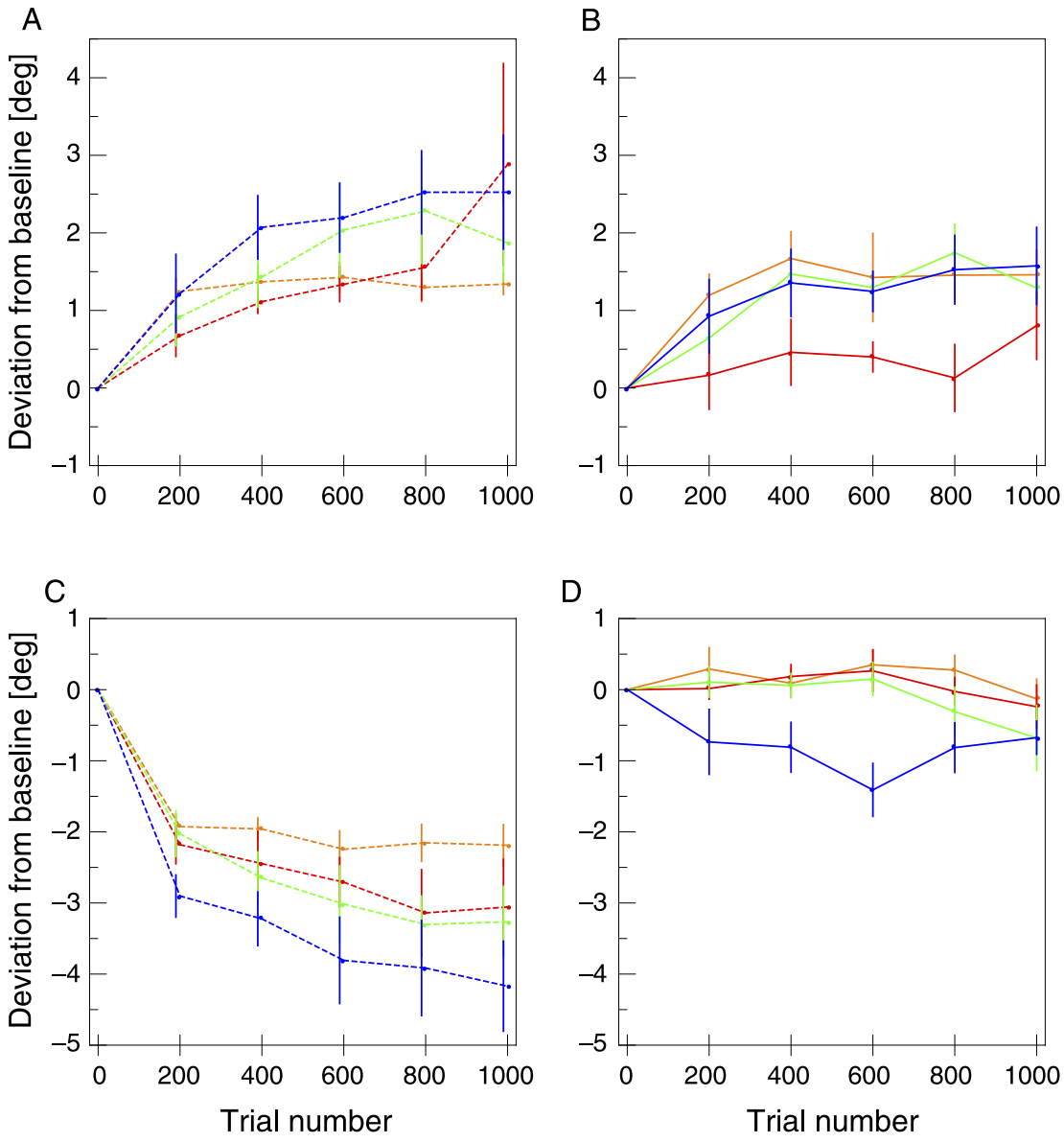

Figure 5. Adaptation (dashed lines) and mislocalization (solid lines) obtained with the constant visual error method. The curves show averages and standard errors over subjects for adaptation with 1 deg visual error (red), 2 deg visual error (green), and 3 deg visual error (blue). For comparison, mean curves from adaptation with the normal adaptation method are shown in gray. (A, C) Outward adaptation. (B, D) Inward adaptation.

Peak velocities of adapted and mimic saccades (1 deg: adap = 451.5 deg/s (*SE* 26.9 deg/s), mimic = 474.9 deg/s (*SE* 21.9 deg/s); 2 deg: adap = 472.6 deg/s (*SE* 26.6 deg/s), mimic = 479.1 deg/s (*SE* 12.7 deg/s); 3 deg: adap = 455 deg/s (*SE* 16.2 deg/s), mimic = 462.1 deg/s (*SE* 9.2 deg/s)) were not significantly different in any of the conditions (one-tailed paired *t*-tests, $p > 0.05$) for outward adaptation. Similarly, peak velocities between adapted and mimic saccades (1 deg: adap = 330.3 deg/s (*SE* 10.8 deg/s), mimic = 313.6 deg/s (*SE* 14.7 deg/s); 2 deg: adap = 324.5 deg/s (*SE* 12.3 deg/s), mimic = 311.1 deg/s (*SE* 16.8 deg/s); 3 deg: adap = 350.1 deg/s (*SE* 18.8 deg/s), mimic = 330.1 deg/s (*SE* 8.2 deg/s)) were not significantly different in any of the conditions (one-tailed paired *t*-tests, $p > 0.05$) for inward adaptation.

This suggests that the constant post-saccadic error condition induced a contribution of target remapping not only for outward but also for inward adaptation.

Discussion

Our results show that modifications in motor parameters as induced by saccadic adaptation change the localization

of visual objects in space. Perceptual localization was shifted after motor adaptation even when the subject continuously fixated during the localization task. The localization changes are thus a consequence of the saccade adaptation procedure and cannot be explained by changes in motor performance, or by mismatches between the saccade and its related efference copy signals. The changes of visual localization that are brought about by saccadic adaptation therefore imply a contribution of saccade motor parameters to visual space perception. A large and enduring post-saccadic error was required for the development of localization changes. In the normal adaptation procedure of McLaughlin's (1967) paradigm, mislocalization occurred only after outward, and not after inward, adaptation. In inward adaptation, the post-saccadic error reduces quickly in the first few trials. Outward adaptation is slower and less complete than inward adaptation resulting in a larger post-saccadic error that is retained for a longer number of trials. When we introduced a permanent post-saccadic error of 3 deg for inward adaptation with the constant error method (Robinson, Noto, & Bevans, 2003), a change in visual localization was induced also for inward adaptation.

Why does the amount of localization change depended on the size of the post-saccadic error?

The generation of a saccade is a complicated process that requires the concerted action of a network of brain areas including visual, parietal, and frontal cortices, the superior colliculus, the cerebellum, and the brain stem. Adaptation experiments with different saccade types (Alahyane et al., 2007; Deubel, 1995; Panouilleres et al., 2008; Zimmermann & Lappe, 2009), as well as electrophysiological (Catz, Dicke, & Thier, 2008; Takeichi, Kaneko, & Fuchs, 2005, 2007) and lesion (Alahyane et al., 2008; Gaymard, Lynch, Ploner, Condy, & Rivaud-Pechoux, 2003; Straube, Deubel, Ditterich, & Eggert, 2001) studies have shown that adaptation can take place at multiple stages of the oculomotor transformation. Based on such evidence, a cerebellar gain learning stage where saccade amplitudes are adaptively tuned has been distinguished from a target representation stage where saccade target representations are modified (Gancarz & Grossberg, 1999). Recent investigations of the time course of adaptation (Ethier et al., 2008; Xu-Wilson, Chen-Harris, Zee, & Shadmehr, 2009) and of the dynamics of adapted saccades (Chen-Harris et al., 2008; Ethier et al., 2008) also distinguished adaptation of motor performance via changes to internal monitoring in a forward model from adaptation due to changes in the motor command, i.e., the target representation.

When a saccade fails to reach its target, the oculomotor system is faced with the problem to decide whether the post-saccadic error is due to an inaccurate motor command or to inaccuracies in the sensory representation of the target (Kording, Tenenbaum, & Shadmehr, 2007). Depending on the outcome of the error assignment, different stages of the oculomotor transformation are modified. The probability to assign errors to the target representation stage rises with increasing post-saccadic error (Chen-Harris et al., 2008; Ethier et al., 2008). Inward adaptation, in which errors were reduced quickly, should, therefore, rely more on gain learning, and outward adaptation, in which error reduction was less complete, should induce changes in the saccade target representation. Since gain learning modifies saccade dynamics, peak velocities of adapted saccades should be different from peak velocities of unadapted saccade of the same amplitude (Ethier et al., 2008). Indeed, the peak velocities of saccades adapted in inward direction were reduced compared to peak velocities of same-amplitude unadapted saccades. However, the peak velocities of saccades adapted in outward direction were nearly identical to peak velocities of unadapted saccades of the same amplitude. Therefore, saccade amplitude decreases induced with the normal adaptation method are very likely to be induced with a gain learning mechanism. Amplitude increases, however, might be due to a change in the saccade target representation and, therefore, would be expected to be associated with visual localization.

Size and persistence of the post-saccadic visual error

The occurrence of induced shifts of visual localization is related to the size and persistence of the post-saccadic visual error. For outward adaptation, constant post-saccadic errors of 2 or 3 deg, which were applied with the constant visual error adaptation method induced changes of visual localization, whereas a constant post-saccadic error of 1 deg did not. For inward adaptation, a constant post-saccadic error of 3 deg induced localization changes, but smaller post-saccadic errors did not. This dependence on post-saccadic error might explain why in the normal adaptation condition changes in localization were only observed in outward and not in inward adaptation. In inward adaptation, which is faster than outward adaptation, the reduction of saccade amplitude that is accomplished via modifications to the saccade dynamics within a few tens of trials is already strong enough to lower the post-saccadic error to below 1 deg. The remaining error is too small to drive further adaptation (i.e., the adaptation levels asymptotically) or any target remapping. For outward adaptation, which is slower and less efficient, the post-saccadic error remains high for a large number of trials—even after 1000 trials, it is still 1.6 deg—and is large enough to require target remapping and induce localization changes. Only the

target representation stage would be expected to be associated with visual localization. Adaptation at other levels should take place without influences on localization. We believe that mislocalization occurred only in outward adaptation or in adaptation with larger constant visual errors since only large and permanent post-saccadic errors induce changes in the saccade target representation. The analysis of peak velocities supports this. Contrary to the standard inward adaptation, peak velocities for inward adaptation with a constant post-saccadic error were not reduced, suggesting that inward adaptation in the constant error paradigm includes a component of target remapping. However, even with a constant post-saccadic error mislocalization for outward adaptation is still larger than in inward adaptation with a constant post-saccadic error. This result suggests that inward adaptation with a constant post-saccadic error might be achieved by a mixture of changes in the saccade dynamics and changes in the saccade target representation. In the peak velocity analysis, these changes might be too small to become significant. Another reason why inward adaptation is different from outward adaptation might be that the oculomotor system expects a post-saccadic error after each saccade. Since saccades usually undershoot their targets, the oculomotor system would expect to land to the left of the saccade target. A displacement of the saccade target in the outward direction would be in the same direction as the expected post-saccadic error and could therefore be not as efficient as a displacement in inward direction. An interesting question is whether the post-saccadic error has not only to be large but also to be consistent to induce changes in the saccade target representation. To answer this question, one could add randomly a trial-by-trial variability to the constant error such that it has always a minimum size but is not consistent over the trials.

Comparison to previous studies

Consistent with this, earlier studies that used only rapidly adapting inward adaptation or small target steps reported only small (Moidell & Bedell, 1988) or insignificant localization changes during fixation (Awater et al., 2005; Collins et al., 2007). Our experiments showed large and significant localization changes because we used larger post-saccadic errors and examined outward and inward adaptations. A transfer of saccadic adaptation to pointing movements for outward but not for inward adaptation (Hernandez et al., 2008) is also consistent with this interpretation. Differences between gain increasing and gain decreasing adaptations were furthermore described in a study in which amplitudes of normal saccades were adapted, and the transfer of adaptation to anti-saccades in the same and opposite directions was measured (Panouilleres et al., 2008). Specifically, anti-saccades in the opposite direction provide an indication of adaptation in the target localization stage because these anti-saccades are instructed by the same target as the normal saccade but are executed in the opposite direction. Adaptation in the motor stage of saccade execution should, therefore, not have an effect on these saccades. Indeed some subjects of Panouilleres et al. (2008) showed transfer to opposite anti-saccades for gain increasing but not for gain decreasing adaptation.

Influences of saccade adaptation on visual localization have previously been demonstrated in studies in which subjects reported the perceived probe position after performing an adapted saccade (Awater et al., 2005; Bahcall & Kowler, 1999; Bruno & Morrone, 2007; Georg & Lappe, 2009). The results of these studies are consistent with an adaptation of the target representation, but they also allow an alternative explanation in which mislocalization occurs because the perceptual system uses an efference copy signal for trans-saccadic remapping that is not adapted. Because the unadapted efference copy is not a faithful representation of the actual, adapted, saccade, pre-saccadic stimuli are mislocalized after the saccade in amount of the difference between efference copy and actual saccade. The mislocalization in the present study cannot be explained by erroneous efference copy because in the localization trials no saccade was performed and no efference copy signals were involved. Our data thus support only the target adaptation explanation.

The efference copy explanation, moreover, has difficulties to explain the correlation of mislocalization and adaptation. First, mislocalization is restricted to the spatial adaptation field surrounding the adapted saccade (Collins et al., 2007). The efference copy explanation, however, would predict a uniform shift over the whole visual field. Second, the finding that the adaptation-induced mislocalization is selective for the types of saccades adapted and the temporal properties of stimuli that have to be localized (Zimmermann & Lappe, 2009) is difficult to explain with an efference copy. Because adaptation of reactive saccades induced mislocalization of flashed probes and adaptation of scanning saccades induced mislocalization of flashed and stationary probes, an efference copy explanation would require different efference copies for different saccade types and specific interactions of these efference copies with the specific visual stimuli.

Conclusion

We conclude that consistent visual indications of large oculomotor errors induce not only adaptations of the motor commands but also affect visual perception of location. Thus, visual localization is not simply based on retinal signals but takes into account the sensorimotor contingencies of reaching for a location with an eye movement. Such a coupling of localization and saccade

targeting may occur if perceptual localization is based on activities in oculomotor maps. Indeed, it has been proposed that our perceptual experience of the world is composed of the sensorimotor transformation laws that govern how we interact with the world (O'Regan & Noe, 2001; Varela, Thompson, & Rosch, 1992). Alternatively, the brain may keep visual and oculomotor maps in register by updating visual representations when eye movements consistently fail to reach the target. Using the same spatial map for sensory and motor processes has the advantage that perception and action are instantaneously aligned onto each other. A perceptual map that is not updated of modifications of motor metrics would lead to discrepancies between perceptual and motor targeting, which would be calamitous in everyday action.

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