Saccade adaptation goes for the goal

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The oculomotor system maintains saccade accuracy by adjusting saccades that are consistently inaccurate. Four experiments were performed to determine the relative contribution of background and target postsaccadic displacement. Unlike typical saccade adaptation experiments, we used natural image scenes and masked target and background displacements during the saccade to exclude motion signals from allowing detection of the displacements. We found that the background had no effect on saccade gain while the target drove gain changes. Only when the target was blanked after the saccade did we observe some adaptation in the direction of the background displacement. We conclude that target selection is critical to saccade adaptation, and operates effectively against natural image backgrounds.

Introduction

Saccades are the fast movements of the eyes used to explore the visual environment and to react to displacements of visual objects. When the relation of the target and fovea is changed, for instance, by introducing an intrasaccadic step such that the target is surreptitiously moved while the eye is in flight, the oculomotor system is able to adapt the amplitude of saccades (McLaughlin, 1967). This saccade adaptation is a form of motor learning that maintains accuracy in response to new sensorimotor contingencies. We have recently demonstrated that in the presence of two competing visual stimuli, a target and a distractor, the saccadic system selectively adapts its gain as though only the target were present (Madelain, Harwood, Herman, & Wallman, 2010). We proposed that the saccadic system selectively uses the signal originating from the target to change its gain, while ignoring the one related to a distractor. The role of target selection in saccade adaptation is usually overlooked in the laboratory by using single targets over an empty background because this impoverished visual environment provides a unique postsaccadic position error signal to drive adaptation in saccade amplitudes. However, in real life, complex structured visual backgrounds are present and provide myriad possible competing error signals that could drive adaptation: A hypometric saccade would undershoot not only the intended target but the entire background as well. On the one hand if saccade adaptation does not rely on target selection but is rather a simple motor calibration mechanism, saccade adaptation should be much stronger when a background image is displaced intrasaccadically with the saccade target than when a single spot is used because the perceived error signal should be larger and more consistent when the background is also displaced. On the other hand, if saccade adaptation relies on target selection, changes in saccade amplitude should be independent from intrasaccadic background displacement and rely exclusively on the postsaccadic target position error signal.

Despite a large number of studies dedicated to describe saccade adaptation (see Hopp & Fuchs, 2004; Pélisson, Alahyane, Panouillères, & Tilikete, 2010)

there are surprisingly few data probing the effects of backgrounds. In humans only two sets of studies addressed these issues (Deubel, 1995; Ditterich, Eggert, & Straube, 1999, 2000). Deubel showed that a static background does not prevent adaptation. Ditterich et al. report that intrasaccadic displacement of a visual background did not influence the saccade gain. However, in these experiments there was no attempt to disentangle the relative contribution of an intrasaccadic target shift and an intrasaccadic background shift to saccade adaptation. Moreover, the background consisted in sparse white disks displayed over a black screen, providing a somehow uniform image, because the goal of this study was to probe the role of attentional focus on saccade adaptation rather than the effect of a complex structured natural image (Ditterich et al., 2000; Figure 1). In monkeys, Robinson, Noto, and Watanabe (2000) used real-world images such as astronomical objects or a man walking in the forest as backgrounds over which a spot was projected. Surprisingly, they observed that when moving the background with a target spot during backward adaptation trials the amount of change in saccade gain was less than when using a back-stepping target with no background. More generally they reported that background movements had no effects on saccade adaption which rather followed the target's intrasaccadic movements. However, in the background-displaced conditions the authors chose to have the background move not only during the saccade but also stepping with the target to trigger the initial saccade (their figure 2B, D). Therefore monkeys saw the entire visual field abruptly displaced by up to 20° while they were fixating, a situation which induces large visual transients that may have considerably reduced the effects of postsaccadic visual error signals originating from the background. Finally, in all these experiments the background displacements presumably induced strong motion signals that may have biased the competition between the target and background position error signals. It therefore remains unknown whether saccade adaptation in the presence of a natural image background depends on motion signals originating from the intra-saccadic scene displacement. Moreover, the relative contribution of background and target is obscure and disentangling the role of each signal may provide critical knowledge on transsaccadic comparison mechanisms for adaptation.

Here, we have modified the conventional double steps paradigm by having a target appearing in the periphery over a static natural image. Depending on the experiment, the target or the background remained static or were displaced at saccade offset and a whole-field mask was displayed during the saccade to limit the possible contribution of motion signals. Our results support the view that, when present after the saccade, it is the target—not the background—that causes changes in saccade amplitude. When the target is extinguished upon saccade, however, displacing the background does trigger saccade adaptation.

Methods

General methods

Four experiments tested the relative contribution of a target and a natural background image on saccade adaptation. Each trial started with a fixation period of 750–1250 ms during which a fixation target (a white disk, 0.16° diameter) was displayed about 8° either above, below, to the left, or to the right of the center of the screen against the natural image of a forest (Figure 1B) encompassing the entire screen. If fixation was broken, i.e., if the eye position was not in a 2 × 2° square centered on the fixation target location at the end of the fixation period, the background image was turned off and the fixation target was displayed for 500 ms against a gray background before starting the whole fixation period again. After this fixation period, an auditory tone sounded, the fixation target disappeared, and a saccade target appeared 11.5° away from the fixation position (Figure 1A). To ensure short saccadic latencies, trials in which no saccade was detected 400 ms after target onset were cancelled (3.96% of trials on average). At saccade onset a mask image (a scrambled version of the background image, formed by randomly changing the positions of 2° × 2° portions of the image) was displayed until the offset of the saccade was detected. Then, depending on the actual experiment, the background image and the target could either reappear at the presaccadic location or displaced toward the initial fixation position by 1.73° (15% of the original target eccentricity). This intrasaccadic mask was used in order to prevent the motion signals resulting from the scene displacement. In other words, this paradigm allowed us to independently manipulate the postsaccadic error signals induced either by the background image or the saccade target. After 300 ms, 10 mask images (scrambled versions of the background image, formed by randomly changing the positions of 2° × 2° portions of the image) were successively displayed for 20 ms each. Then the background image reappeared, centered with respect to the center of the screen and remained visible until the beginning of the next trial. The purpose of masking the background image with a dynamic mask was to precisely control the duration of exposure to the postsaccadic scene while avoiding a possible after image that would result by simply turning off the image. The saccade target consisted of a rectangular portion of the background
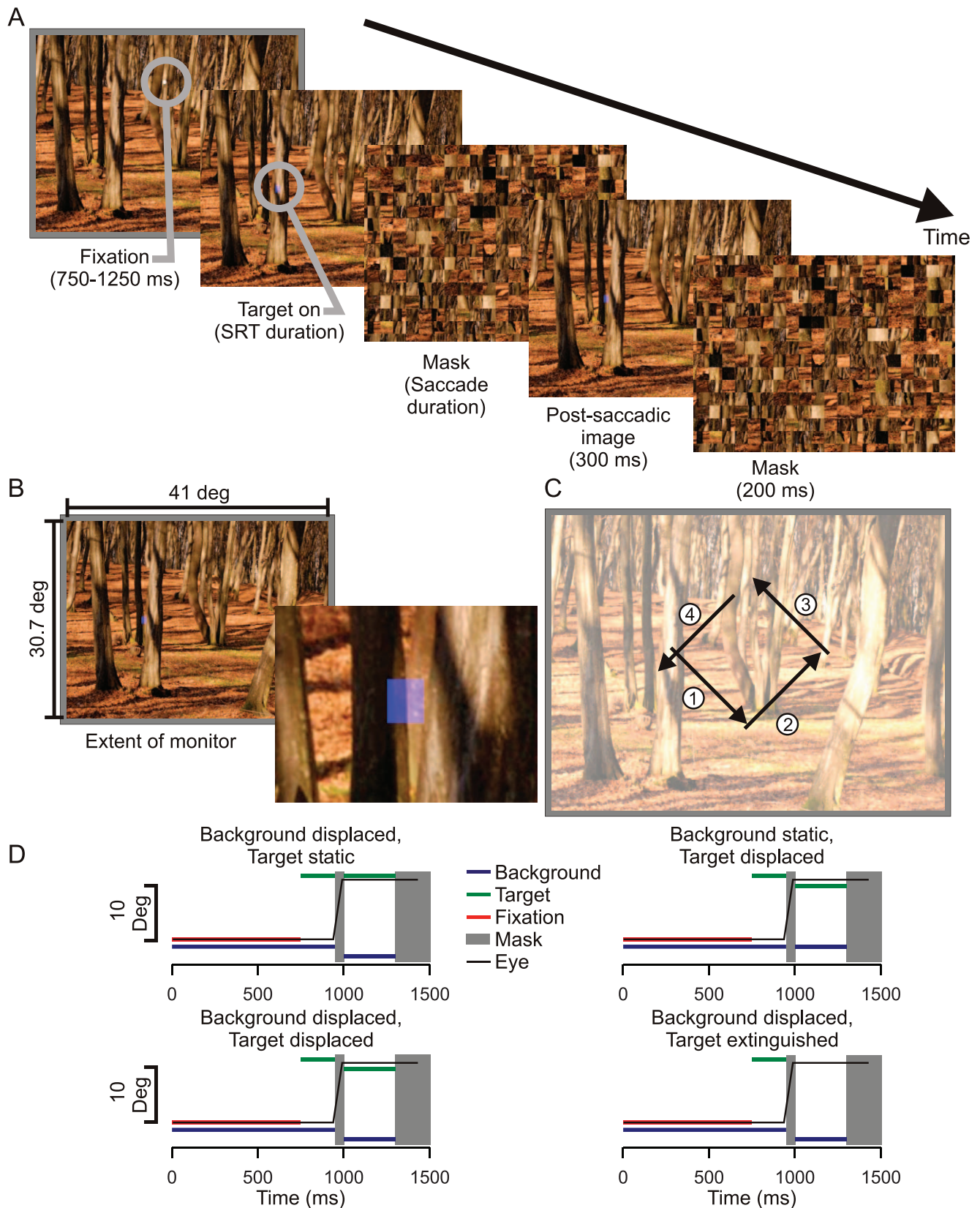
Figure 1. (A) Schematic diagram of the time course of one trial. The gray rings indicate where the fixation disk and target are but were not displayed in an actual experiment. (B) Example of a vertically-orientated target displayed over the background image. (C) Schematic example of four target vectors in a four-trials block. (D) Example of possible time course of events in each experimental paradigm during an adaptation trial. Note that in an actual experiment the precise time course depended on both the saccadic reaction time and saccade duration. Blue, background position; red, fixation target position; green, saccade target position; black, eye position. Gray areas indicate that a randomly scrambled version of the background image was displayed.

image in which the blue gun was turned up so that the target appeared like a blue transparent rectangle over the background. The size of the target was either 0.4° × 0.49° (vertical target) or 0.49° × 0.4° (horizontal rectangle; Figure 1B). Saccades were detected online using a 30°/s velocity threshold (the average delay between the actual onset and offset of the saccade and its online detection was 24 ms as revealed by offline data analysis).

To ensure that subjects would saccade to the target and not to a feature of the background, we used the orientation of the target as a stimulus for a psychophysical task. All experiments consisted of 200 blocks of four trials. The beginning of each four-trial block was signaled by having the fixation target color alternating between blue and white for 400 ms at a frequency of 20 Hz prior to the fixation period. In half of the blocks, the targets positions were such that the subjects had to make four saccades in the counterclockwise direction around the center of the screen (Figure 1C) while, in the other half, the direction was clockwise. The direction was randomly assigned at the beginning of each block. On each trial, the position of the fixation disk was randomized by adding independent random values from a flat distribution ranging from −1° to +1° to the horizontal and vertical positions. The number of vertical targets in each block randomly varied between one and four. Subjects were instructed to first fixate the fixation target and then make a saccade to the blue rectangle as soon as they detected it. In some experiments (see below) subjects were also instructed to perform a psychophysical task in addition to the saccade task to ensure that the postsaccadic target was attended. This psychophysical task consisted in reporting at the end of each block of four trials the number of saccade targets that were vertical (either one, two, three, or four) using a keyboard. An auditory tone and text feedback signaled correct reports.

Experiment 1: Background displaced, target static (BdTs)

The first experiment tested whether decreased saccade amplitude would result from backward postsaccadic displacement of the background image if the saccade target position remained unchanged after the saccade (Figure 1D, top left). Each subject experienced three experimental conditions within a single session: first subjects performed 200 pre-adaptation trials in which both the background image and the target reappeared at their presaccadic locations when the offset of the saccade was detected (i.e., after a scrambled version of the image was displayed as a mask). Then 400 adaptation trials, in which the target reappeared at its presaccadic location and the back-

ground image was moved toward the initial fixation position by 1.73° (15% of the original target eccentricity). Finally 200 recovery trials, in which both the background image and the target reappeared at the presaccadic location, were recorded. Subjects were instructed to report the number of vertical targets seen within each block of four trials.

Experiment 2: Background static, target displaced (BsTd)

The second experiment tested whether decreased saccade amplitude would result from backward postsaccadic steps of the saccade target while the background image position remained unchanged (Figure 1D, top right). In the 200 pre-adaptation trials both the saccade target and the background image reappeared at their presaccadic locations. In the 400 adaptation trials the saccade target was moved toward the initial fixation position at saccade offset by 1.73° and the background image reappeared at the presaccadic position. Finally the recovery trials were identical to the pre-adaptation trials. At the end of each block of four trials, subjects performed the psychophysical task.

Experiment 3: Background displaced, target displaced (BdTd)

In a third experiment we asked whether saccade amplitude would change in the case of a postsaccadic displacement of both the target and background image (Figure 1D, bottom left). The pre-adaptation and recovery trials were identical to the ones in Experiments 1 and 2. In the adaptation trials both the background image and the target were moved toward the initial fixation position at saccade offset by 1.73°. Two hundred recovery trials, identical to the pre-adaptation trials were then recorded. Subjects performed the psychophysical task throughout the experiment.

Experiment 4: Background displaced, target extinguished (BdTe)

In a fourth experiment we asked whether postsaccadic displacement of the background image would affect saccade amplitudes in the absence of an explicit postsaccadic target (Figure 1D, bottom right). In this experiment, the target was systematically extinguished when the offset of the saccade was detected (i.e., after a scrambled version of the image was displayed as a mask). Subjects were not instructed to report the number of vertical targets seen within each block of

four trials but instead to only make a saccade toward the target location.

In the 200 pre-adaptation trials and 200 recovery trials the background image position remained unchanged throughout the trials. In the 400 adaptation trials the background image was moved toward the initial fixation position at saccade offset by 1.73°.

Participants

Six subjects each performed all of the experiments. Two were naïve as to the purpose of the experiments, but had previous experience in oculomotor experiments (subjects S1 and S3), three never experienced eye movement recording (subjects S4, S5, and S6), and one was author of the study (subject S2). All had normal vision. Subjects first carried out a training session of 800 trials to become familiar with the requirements of the experiment and with the psychophysical task. The order of the four experiments was randomized across subjects. Subjects performed two sessions per week separated by at least 3 days to reduce the possibility that changes in gain may be carried over across sessions. Written consent was obtained from all subjects, and the experimental protocol was approved by the Institutional Review Board.

Apparatus

Subjects in a darkened room viewed stimuli at a distance of 57 cm while on a head and chin rest to minimize head movements. Stimuli were generated on a computer using the Psychophysics toolbox (Brainard, 1997; Pelli, 1997) in Matlab (The Mathworks Inc., Natick, MA) and displayed on a 21-inch ViewSonic Professional Series P227f screen (1024 × 768 pixels at 100 Hz) CRT display (ViewSonic, Walnut, CA). Right eye position was recorded by an Eyelink 1000 (SR Research Ltd, Osgoode, Ontario, Canada).

Data analysis

All analyses were performed using MATLAB (The MathWorks). During offline analysis saccades were first detected automatically using a velocity and an acceleration threshold (22°/s and 3800°/s, respectively). An interactive program presented the start and end of each saccade immediately following the target step to the investigator for confirmation. Trials in which the gain (gain = saccade amplitude/target step) was below 0.5 or above 1.5 or the latency shorter than 100 ms were discarded (on average 2.8% of the saccades were discarded).

To describe the changes in amplitude we computed the mean gain (and standard deviation) of the last 100 trials at each phase (pre-adaptation, adaptation, recovery). Individual *t*-tests were computed to compare the pre-adaptation and adaptation mean gains in each experiment. To show the trends of the changes in gain within individual experiments, we smoothed the records of saccadic gain versus trial number by means of a Lowess iterative nonlinear regression (span = 50 trials), separately for each phase of the experiment. Individual pre-adaptation gains were compared across experiment using a one-way ANOVA and post-hoc all-pairwise comparisons. Finally percent change in gain was computed by dividing the difference between gain in each of the last 100 adaptation trials and the average gain in the last 100 pre-adaptation trials by the average gain in the last 100 pre-adaptation trials.

Results

Our results show that saccade gain changes according to the target postsaccadic position and ignores the background image displacement, unless the target image is extinguished at saccade offset: Saccade adaptation occurred in BsTd, BdTd and BdTe experiment but not in BdTs experiment.

Experiment 1: Background displaced, target static (BdTs)

This experiment measured the changes in saccadic amplitude when the postsaccadic position of the target remained unchanged and the background image was moved across the saccade. Figure 2A plots the saccadic amplitude (in gain units) for a single subject (S1). Throughout the experiment the saccadic gain remained high despite some intertrial variations: At the end of the pre-adaptation trials and at the end of the adaptation trials, the mean saccadic gain was 0.98, well within the range of gains reported in the literature. The gain slightly increased during the 200 recovery trials, as indicated by a raise in the Lowess curve, to reach 1 at the end of the experiment. A similar pattern, i.e., a lack of change across trial types, was found in all subjects, as revealed by the Lowess fits (Figure 2B). It should be noted that one subject (S4, black curve) had a gain slightly lower than the other subjects (0.89 on average throughout the session). Across subjects the gains remained similar in all three trial types (averaging respectively 0.94, 0.95, and 0.95 at the end of the pre-adaptation, adaptation, and recovery trials). To evaluate the effects of the postsaccadic background displacement on saccadic gains, we compared the gains
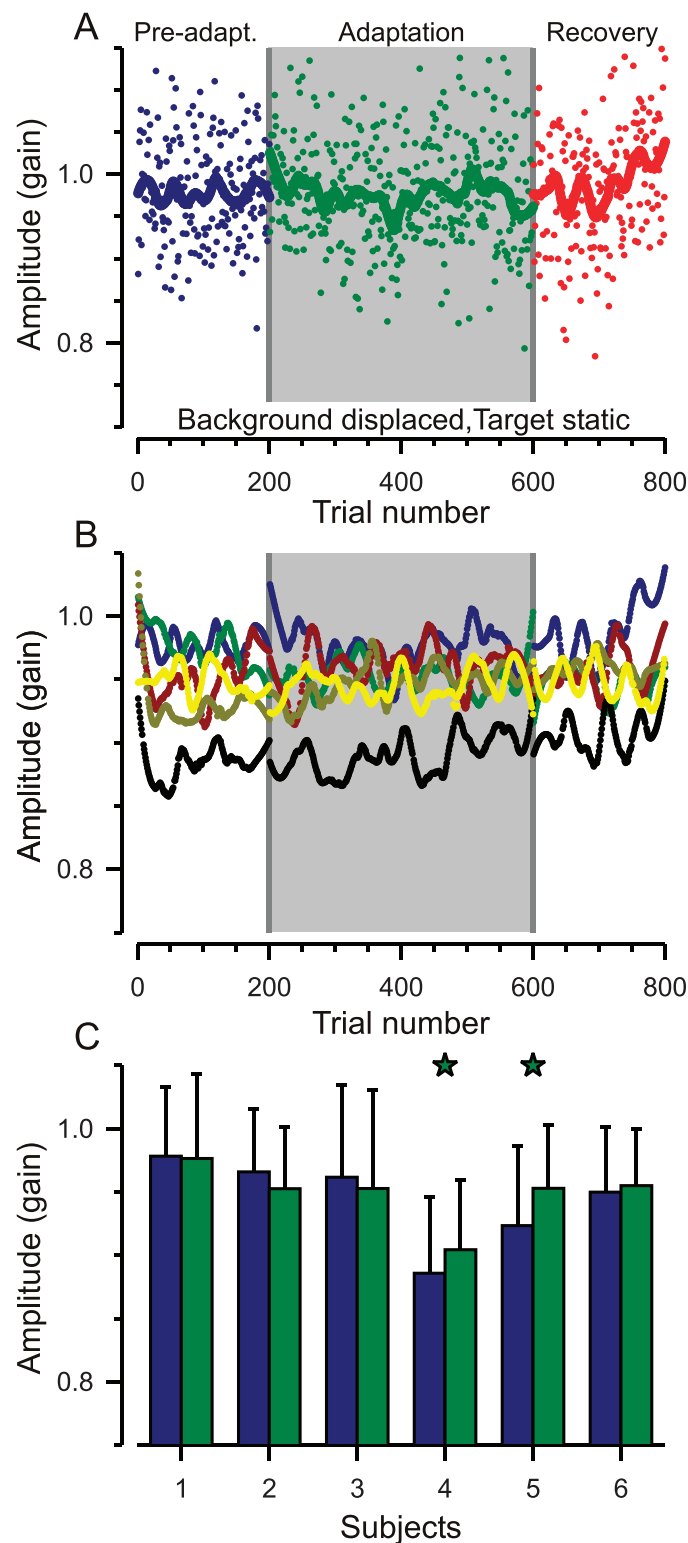
obtained in the last 100 pre-adaptation and adaptation trials using individual t tests (Figure 2C). The trial types had a significant effect in only two subjects (S4 and S5, $p < 0.05$) and these gain changes were in the opposite direction to the background displacement. These increases in gain were small (from 0.89 to 0.90 and from 0.92 to 0.95 for subjects S4 and S5, respectively), and were found in the subjects with the lowest pre-adaptation gains.

Experiment 2: Background static, target displaced (BsTd)

In this experiment the background remained static and the target was displaced after the saccade toward the initial fixation position as in a conventional backstep saccade adaptation paradigm. Figure 3A plots the saccadic gain for subject 1. As revealed by the Lowess curve, the gain slightly increased during the pre-adaptation period to reach 0.98 and then decreased during the adaptation trials. At the end of these adaptation trials the average gain was 0.85. During the recovery trials, i.e., when the postsaccadic target remained at its previously occupied location, the gain increased back to reach 0.93. A similar decrease was observed in all subjects during the adaptation trials (see Lowess curves, Figure 3B): gain decreased from 0.94 in the pre-adaptation trials to 0.86 (average percent change $= -8.9\%$) in the adaptation trials and increased back to reach 0.90 on average in the recovery trials. Individual t-tests comparing the average gains in the pre-adaptation and adaptation trials revealed a systematic significant decrease (Figure 3C, $p < 0.05$).

Experiment 3: Background displaced, target displaced (BdTd)

The goal of this experiment was to probe the effect of a postsaccadic displacement of the background image on the change in gains induced by the postsaccadic target displacement. Much as in the previous experiment we observed a continuous decrease in gain during the adaptation trials (Figures 4A, B) followed by an increase during the recovery trials (from 0.94 in the pre-adaptation trials to 0.86 in the adaptation trials— average percent change $= -9.4\%$—and 0.89 on average in the recovery trials). Individual t-tests revealed

Figure 2. Background displaced, target static (Experiment 1). (A) Individual saccade amplitudes (expressed as gain) for all trials (subject S1). Blue dots, pre-adaptation trials; green dots, adaptation trials; red dots, recovery trials; solid lines, corresponding saccadic gain fit by Lowess smoother. Vertical gray lines mark the transition between phases. Shaded area indicates the adaptation phase. (B) Individual saccadic gain fit by Lowess smoother for all subjects: Blue, S1; green, S2; red, S3; black, S4; brown, S5; yellow, S6. (C) Individual mean gains and standard deviations for the last 100 pre-adaptation (blue) and adaptation (green) trials. Stars indicate statistically significant differences (corrected t-tests, $p < 0.05$).
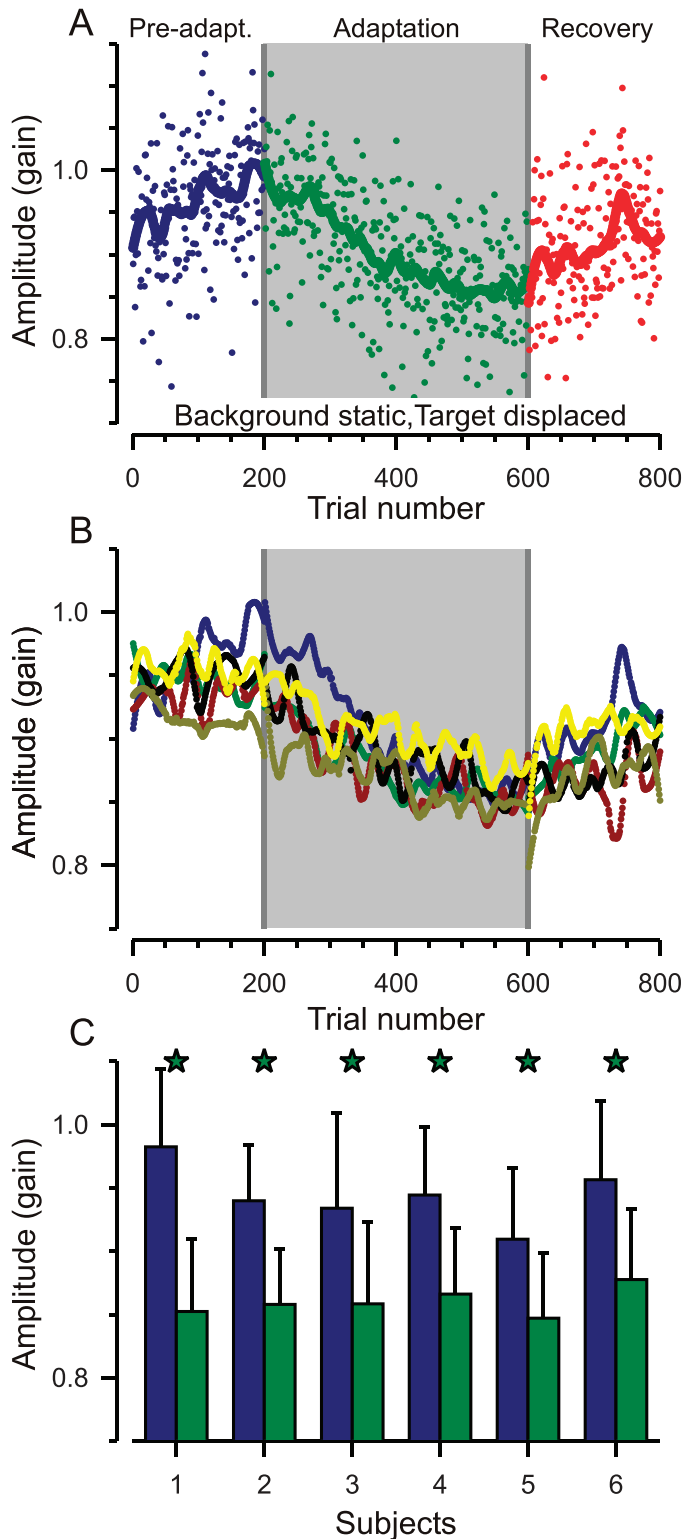
Figure 3. Background static, target displaced (Experiment 2). (A) Individual saccade amplitudes (expressed as gain) for all trials (subject S1). (B) Individual saccadic gain fit by Lowess smoother for all subjects. (C) Individual mean gains and standard deviations for the last 100 pre-adaptation and adaptation trials. Symbols and colors as in Figure 2.

significant decreases in gain in all subjects (Figure 4C, $p < 0.05$).

Experiment 4: Background displaced, target extinguished (BdTe)

The last experiment tested whether saccade adaptation might be induced by changing the postsaccadic position of the background image in the absence of a postsaccadic target. In subject 1 (Figure 5A), the gain slightly decreased during the adaptation trials from 0.97 to 0.91, and then slightly increased back to reach 0.93 at the end of the recovery trials. A similar trend was observed in all subjects (Figure 5B): Across subjects the gain decreased from 0.94 at the end of the pre-adaptation trials to 0.90 at the end of the adaptation trials (average percent change = −4%) and reached 0.91 after recovery. A significant decrease, as revealed by individual t-tests ($p < 0.05$) was observed in all subjects (Figure 5C) except subject S5 (from 0.91 to 0.90, N.S.).

Comparison across experiments

As we just reported, saccade adaption was significant in all subjects in the BsTd and BdTd experiments and in all but one subject in the BdTe experiment. However no reduction in gain was observed when the background but not the target was displaced after the saccade (BdTs experiment). Because the same subjects were tested in all four experiments, it is possible to compare the eye movement behaviors across experiments.

We first compared the saccadic reaction time (Figure 6A) across experiments using individual one-way ANOVAs and all pair-wise post-hoc comparisons. On average latencies were short across subjects and across experiments (164 ms) as required by our paradigm in which trials were interrupted when reaction time exceeded 400 ms. ANOVAs revealed a systematic difference in mean latencies across experiments ($p < 0.05$ in all subjects). However, post-hoc pair-wise tests indicated that the only systematic significant change was an increase between the BdTs and BdTe experiments ($p < 0.05$ in all but one subject, from 159 ms to 176 ms when averaged across subjects). Reaction times were also longer in the BdTe experiment than in the BsTd experiment in four subjects (S1, S2, S3, and S4) and than in the BdTd experiment in three subjects (S3, S4, and S5). This effect may be due to the fact that there was no psychophysical task in the BdTe experiment, therefore reducing the urgency to saccade to the target. However it should be pointed out that the extent of these differences was generally small (average 15 ms). When comparing the latencies of corrective

saccades, i.e., saccades immediately following the first saccade during the adaptation trials, we did not find any consistent differences across conditions (one-way repeated measure ANOVA [3,5], N.S.).

Because the amount of saccade adaptation may be reduced when pre-adaptation gain is low, we next compared the pre-adaptation gain across experiments using individual one-way ANOVAs and post-hoc all pair-wise comparisons (Figure 6B). We found that, although the ANOVAs indicated significant differences in gain in all but one subject (S6), no systematic pattern was present when performing the post-hoc comparisons. For instance the pre-adaptation gain was higher in the BsTd experiment when compared to the BdTd experiment in three subjects (S1, S3, and S4) but the opposite was true in subjects S2 and S5.

Finally we compared the extent of adaptation across experiments using individual one-way ANOVAs on percent change (Figure 6C). For all subjects, we found significant differences between experiments ($p < 0.05$). Given that no adaptation was found in the first experiment, it is not surprising that pair-wise comparisons revealed a systematically significantly ($p < 0.05$) greater change in gain in the BsTd, BdTd, and BdTe experiments when compared to the BdTs experiment (−8.9%, −9.4%, −4%, and 0.6%, respectively in the BsTd, BdTd, BdTe, and BdTs experiments). Moreover, percent changes in gain were significantly higher in the BsTd experiment when compared to the BdTe experiment (except in S2) and in the BdTd experiment when compared to the BdTe experiment. However, we did not observe any systematic trend when comparing BsTd and BdTd experiments: Percent change in gain was significantly less important in the BsTd experiment than in the BdTd experiment for three subjects (S2, S3, and S5) but it was greater in the other three subjects (although significance level was reached only in subject S4).

Discussion

We have shown for the first time that with a cluttered, natural image background present, human saccade adaptation is strongly selective for displacements of the presaccade target goal as opposed to the background. When the postsaccadic target moved, there was equally strong adaptation regardless of whether the background was static or was displaced by the same amount (Figure 6C, BsTd and BdTd). When the target was in the same spatiotopic location after the saccade, but the background image was displaced, there was no adaptation (Figure 6C, BdTs). Finally, when the target was switched off upon saccade, displacements of the entire image caused intermediate levels of
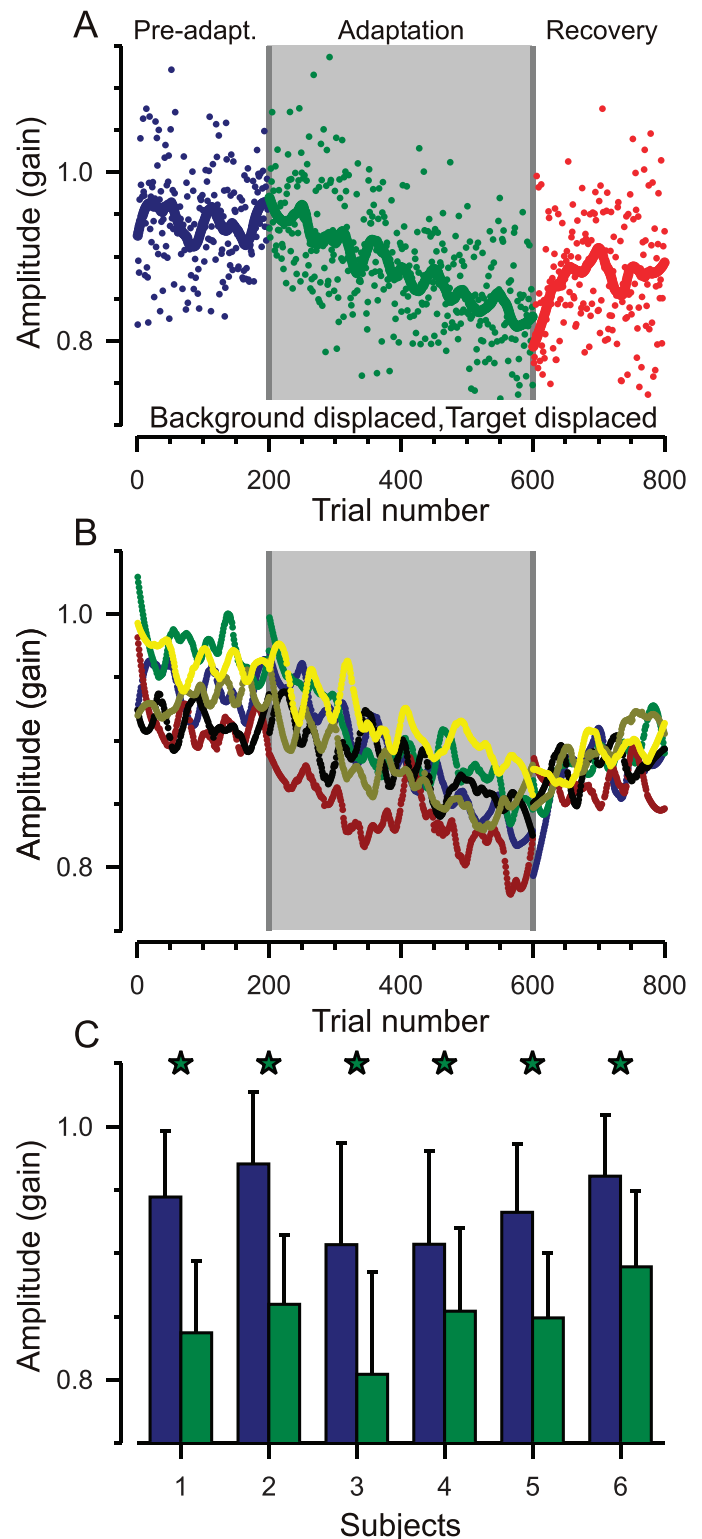

Figure 4. Background displaced, target displaced (Experiment 3). (A) Individual saccade amplitudes (expressed as gain) for all trials (subject S1). (B) Individual saccadic gain fit by Lowess smoother for all subjects. (C) Individual mean gains and standard deviations for the last 100 pre-adaptation and adaptation trials. Symbols and colors as in Figure 2.

adaptation (Figure 6C, BdTe). In addition to the first use of natural images in laboratory saccade adaptation in humans, our key novelties included the use of masking during the saccade and a transparent target, which showed that our effects were purely trans-saccadic and raised issues relating to object and features used by saccade adaptation processes.

Target selection in saccade adaptation

Most adaptation studies have used highly reductionist stimuli, frequently single-spots stepping intra-saccadically on homogeneous backgrounds, and it is a critical open question as to how well these data translate to real-world situations, in which targets are embedded in highly cluttered scenes. The conventional single-spot experiments do not require any target selection after the saccade, whereas in real life the target has to be re-identified amid many competing possible targets. Previously, as a first step in understanding this process, we presented two similar targets postsaccade, and observed that saccade adaptation is highly selective for displacements of the original target (Madelain et al., 2010). That is, retinal error signals from similar competing targets were successfully ignored. The natural image background in the current study presented myriad potential retinal error signals post saccade. When there was a clearly defined postsaccade target that matched the presaccade target (Experiments BdTs, BsTd, and BdTd, Figure 6C), all of these possible local background-derived error signals were successfully ignored in favor of that defined by the pre-saccade goal, which drove the adaptation. In concert with our previous demonstration that adaptation is unhampered by distractors, our data suggest that conventional paradigms of single-spots moving intra-saccadically on blank backgrounds can relevantly be applied to more natural, real-world scenes in which a particular object is targeted.

Ours is the first saccade adaptation study to our knowledge that has actively masked intrasaccadic target and/or background displacements. Although the magnocellular pathway is suppressed during saccades, it has been found that low-frequency motion signals can be detected during saccades (Castet & Masson, 2000). Conscious or unconscious detection of the target displacement may not be consequential for previous saccade adaptation paradigms with small spot targets on blank backgrounds, but might affect adaptation with large low-frequency background images displaced during saccades. Indeed, we have evidence in a nonadaptation study that whole-field displacements during saccades reliably generate corrective saccades in the direction of background displacement regardless of subjects' awareness of the correct displacement (Her-
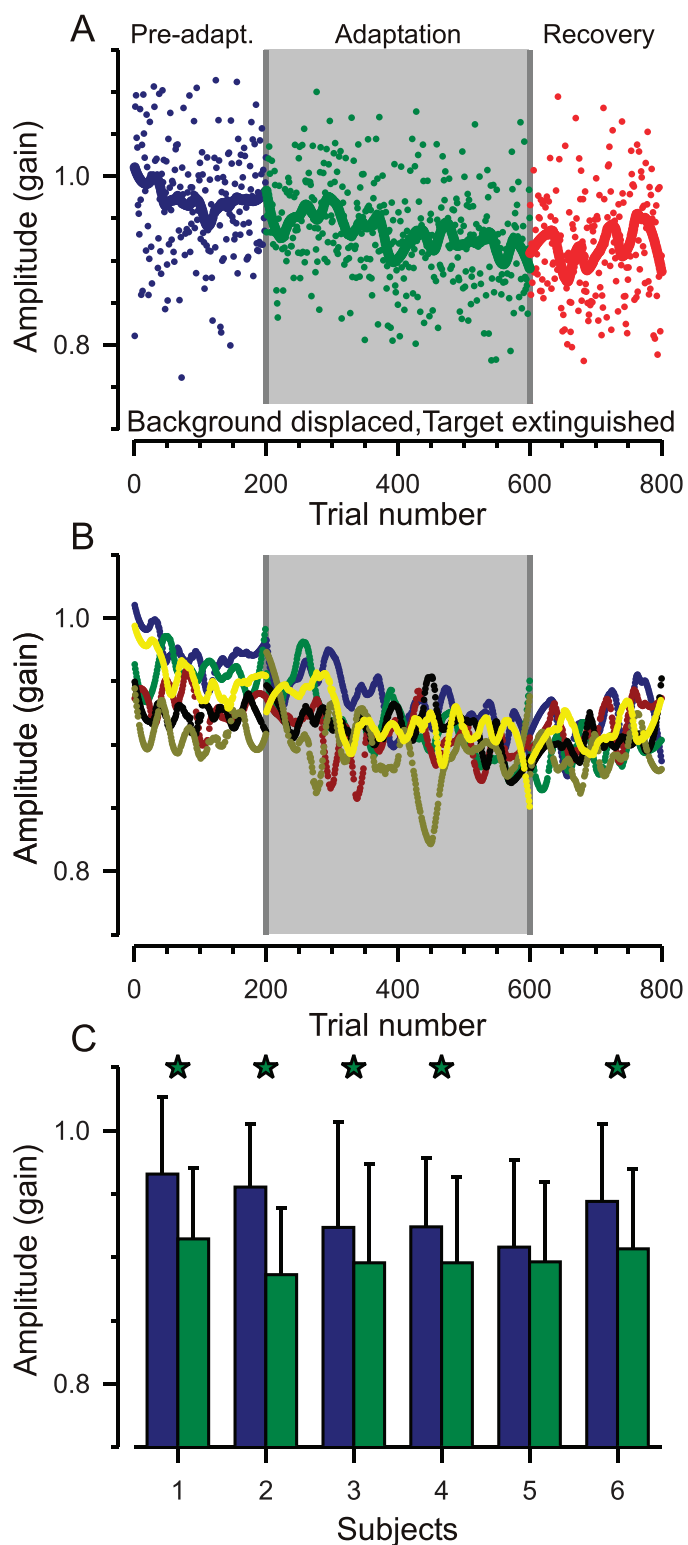

Figure 5. Background displaced, target extinguished (Experiment 4). (A) Individual saccade amplitudes (expressed as gain) for all trials (subject S1). (B) Individual saccadic gain fit by Lowess smoother for all subjects. (C) Individual mean gains and standard deviations for the last 100 pre-adaptation and adaptation trials. Symbols and colors as in Figure 2.
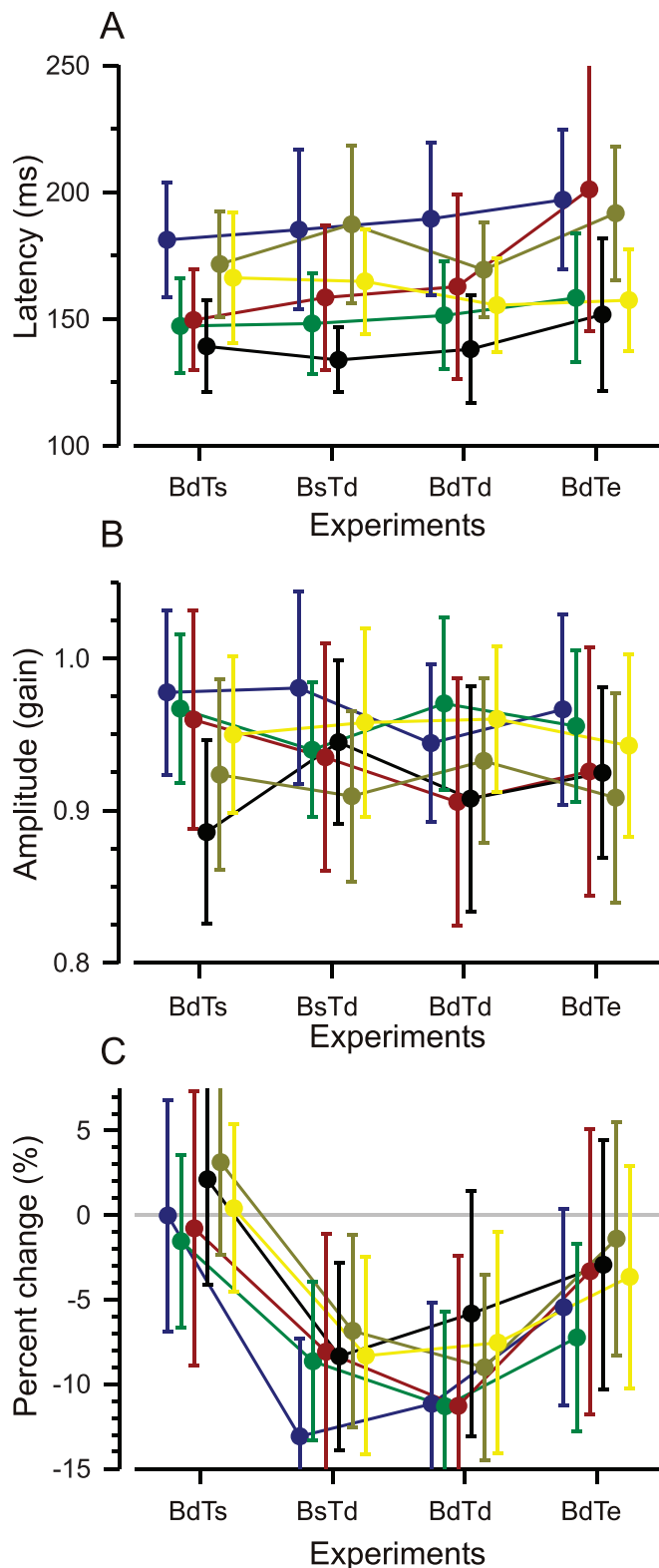
Figure 6. Comparison of experiments. (A) Individual mean saccade latencies and standard deviations (across all trials) for all subjects and all experiments. (B) Individual pre-adaptation mean gains and standard deviations for all subjects and all experiments. (C) Individual mean percent changes in gain and standard deviations for all subjects and all experiments. Colors as in Figure 2.

man, 2012). Hence, we felt it important to control for the possibility that previous studies of background effects during adaptation may have been influenced by intrasaccadic displacements, and dynamically masked all our images during saccades.

Despite this novel masking design, our findings are highly consistent with the few previous reports of adaptation in the laboratory using structured backgrounds. In humans, to our knowledge, only abstract backgrounds have been tested and these have been found to have little effect on adaptation (Deubel, 1995; Ditterich et al., 1999, 2000). Our design was more similar to that tested on monkeys by Robinson and colleagues (2000) as they used a conventional spot target that moved on top of complex images (although, as pointed out in the Introduction, they chose to displace the background before as well as during the saccade, inducing large presaccadic visual transients which may have reduced the efficacy of postsaccadic position signals from the background in causing saccade adaptation). Consistent with our findings, they observed that displacing the background did not affect the amount of adaptation induced by the change in postsaccadic target position, as long as that target was visible immediately after saccade. Moreover, they only found significant effects of the background when it was moved and the spot was switched off upon saccade for 250 ms or 1000 ms, much as in our experiment in which the background was displaced and the target extinguished at saccade offset (BdTe, Figures 5, 6C). It has been previously reported that the visual error driving adaptation is most effective if it occurs within 80–100 ms after the saccade ends both in humans (Bahcall & Kowler, 2000; Fujita, Amagai, Minakawa, & Aoki, 2002) and monkeys (Shafer, Noto, & Fuchs, 2000). Both in Robinson et al.'s data (2000) and in the present study the amounts of adaptation induced by this background displacement (in the absence of a visual target) were smaller than those induced by postsaccadic target displacement. The authors interpreted this outcome as the result of a 'no adaptation necessary' signal from the reappearing target that may have mitigated the effect of the background position error. However this possibility is inconsistent with our own data in which adaptation was reduced even though the target did not reappear (Figures 5, 6C). Instead, we propose that adaptation is driven by a winner-take-all process, which is dominated by the target when present, but this process can also be sensitive to the background when the target is absent. To account for the reduced adaptation from the background position error one may postulate that this signal is intrinsically weaker, for example due to the built-in bias in the visual system towards central vision (M-scaling). Alternatively it could be that the background's features provided a postsaccadic error signal only on a fraction of the

saccades, reducing consistency of the error which is known to weaken adaptation (Havermann & Lappe, 2010). Further support for this possible winner-take-all mechanism comes from the observation that the adaptation induced by the target is not enhanced by background displacement: Overall, we did not find greater adaptation in the BdTd experiment than in the BsTd experiment (compare Figures 3 and 4, and see Figure 6C) much as Robinson et al. (2000) failed to find a linear summation of the background and target error signals.

The lack of linear summation of target and background displacements in these studies is arguably the most significant demonstration of target selection in saccade adaptation. The presumed function of saccade adaptation is usually to recalibrate for neuromuscular changes due to disease, ageing, or fatigue (e.g., Albert, Catz, Thier, & Kording, 2012). These changes would typically affect target and background equally, leading to consistent undershoot or overshoot of both target and background features. Why would the system then choose to ignore information from the vast majority of the visual field in detecting and correcting for inaccuracies? Others have previously suggested that saccade adaptation as typically studied in the laboratory acts for task optimization more broadly, such as efficiently coordinating head and eye movements (Bahcall & Kowler, 2000), rather than purely as a motor recalibration mechanism. Below, we frame this type of task-optimization argument in terms of reinforcing the saccade goal, although this is, of course, not mutually exclusive to a motor recalibration function of saccade adaptation.

Intriguingly, Robinson et al. (2000) also found paradoxical gain increases in some cases to backward displacements of the background, when the target remained static. Although none of our subjects showed backward adaptation in the BdTs experiment, two subjects (S4 and S5) showed some forward adaptation (Figure 2). This is particularly surprising given that gain-increasing adaptation is typically so much harder to elicit with intrasaccadic steps than gain-decrease (Deubel, Wolf, & Hauske, 1986; Miller, Anstis, & Templeton, 1981; Straube, Fuchs, Usher, & Robinson, 1997), and many subjects frequently do not exhibit any gain changes (Erkelens & Hullemann, 1993). Because landmark objects displaced during saccades can induce perceived displacements of static objects (Deubel, 2004), we presume, as did Robinson et al. (2000), that the saccade systems in these subjects interpreted the backward shift of the background as a forward shift in the static target, and thus adapted upwards. Note that these two subjects had lower baseline gains than the others, and so perhaps had "more room" for increasing their gains; further, their onward adaptation still left them with a mean undershoot.

Objects, features, and attention in saccade adaptation

The novel transparency of our adaptation target was designed to put location error signals related to an object (as defined by the rectangular color highlighting) into competition with error signals related to features (in the underlying complex natural image). Clearly, the adaptation machinery treated the highlighting as its target goal irrespective of the underlying features involved since when the highlighting was fixed in space, but the background image was displaced (BdTs), there was no adaptation. Because subjects were instructed to attend to the orientation of the highlighting, and were successful in filtering out task-irrelevant details such as the underlying natural image features, it is tempting to posit a key role for attention in guiding adaptation.

Attention is necessarily deployed to the saccade target before each movement (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995) and is remapped to its expected postsaccadic location (Mathot & Theeuwes, 2010; Rolfs, Jonikiatis, Deubel, & Cavanagh, 2011). Hence, discrepancies between this prediction and the postsaccadic visual information could provide a useful adaptation error signal. Attention acts as a selective filter (Driver, 2001) making it a good candidate for filtering out nontargets from the background in the current study. Ditterich et al. (2000) also interpreted their data in terms of attention playing a key role in adaptation. They argued that when attention was focused on their spot target their structured background was ignored and did not influence adaptation. Conversely, when attention was spread across their 4.8° diameter annulus target, attention was partly on the background, allowing the background to have a small influence on adaptation. Finally, attention can be adapted in a similar manner to saccades, and there is some evidence that this adaptation modifies saccade amplitudes (McFadden, Khan, & Wallman, 2002).

One might argue that the underlying features in our stimuli did not drive adaptation when in competition with the target rectangle, not because they were unattended as task-irrelevant, but because these features were simply too small at the tested eccentricity. Perhaps the features were too small, crowded and nonsalient compared to the highlighting, to act as usefully localizable features presaccade, and in turn for a pre/post saccade detection of displacement that can be used for adaptation. However, displacements of targets defined in a 1-D random grating, which are not perceptually localizable postsaccade, can still induce corrective saccades and adaptation (Deubel, 1991). Moreover, we found significant adaptation when the highlighting was switched off and the background was displaced upon saccade (BdTe). This adaptation could

have been the result of a detection of the local displacement of the object features defined by the presaccade highlighting, although a global detection of image displacement cannot be entirely ruled out. The latter global mechanism is made less likely because we always masked the display during the saccade with a random scrambling of the image, such that large-scale, low-frequency motion signals are unlikely to be responsible for any of our findings.

Our background-induced adaptation with intrasaccadic masking (BdTe) points towards a true transsaccadic comparison of features mechanism driving this adaptation. Others have previously suggested that saccade adaptation might use a low-level correlation mechanism to compare pre- and postsaccadic visual information (Deubel, 1991; Ditterich et al., 1999). These authors invoked correlation to explain their background-induced adaptation, but importantly did not use any form of masking when they displaced their background images during the saccade. Because low-frequency motion signals can be detected during saccades (Castet & Masson, 2000), the adaptation in the previous studies may simply have been driven by an *intrasaccadic* global detection of background image displacement. Our data support a true transsaccadic comparison, but whether it is via an actual correlation, which would be independent of features, or is strongly reliant on transsaccadic feature comparisons, is unclear from our present study.

Is retinal error the signal guiding adaptation?

That target selection is involved in saccade adaptation, as demonstrated both here and in previous research (Madelain et al., 2010), questions the primacy of a strict position error signal for adapting saccade amplitudes (Havermann & Lappe, 2010; Noto & Robinson, 2001; Wallman & Fuchs, 1998). Although these other studies have clearly demonstrated that adaptation is based on visual retinal error signals (not corrective saccade motor errors), it has been previously proposed that failure of predicting the postsaccadic target position is as, or more, important than retinal error (Ditterich et al., 2000; Bahcall & Kowler, 2000; Wong & Shelhamer, 2011). This specialized motor calibration mechanism would compare the expected retinal error based on the programmed saccade with the actual postsaccadic retinal error. In case of prediction error the saccade gain would be progressively adjusted. Importantly, recent data demonstrated that when keeping the trial-by-trial visual position error constant across sessions, saccade adaptation was several-fold greater when the predictability of postsaccadic target position was highly reduced (Collins & Wallman, 2012) supporting this prediction mechanism.

Another argument against raw retinal error as the main signal for saccade adaptation comes from experiments revealing contextual effects on saccade amplitude: Eye position (Alahyane & Pelisson, 2004), head position (Shelhamer & Clendaniel, 2002), target distance (Chaturvedi & van Gisbergen, 1997), or target features (Herman, Harwood, & Wallman, 2009) have been demonstrated to control different adaptation states. Similarly, the maintenance of adaptation despite thousands of unperturbed saccades made between sessions that have been reported in monkeys (Noto, Watanabe, & Fuchs, 1999) and in humans (Alahyane & Pelisson, 2005) may also be explained by contextual effects. The importance of prediction in adaptation is therefore well accepted. However the present results indicate that not all postsaccadic visual information is equivalent in these prediction mechanisms: As we already discussed the postsaccadic image of the background was simply ignored when the target was present. In other words adaptation occurs when the saccade goal, i.e., the landing position with respect to the visual target, is perturbed. In the absence of a specific postsaccadic target, features of the background must define a new goal that controls adaptation.

Reinforcement learning provides a more general mechanism to account for these sensorimotor changes than these specialized motor calibration mechanisms. We have previously proposed that the oculomotor system could increase the probability of saccades that had a better value, i.e., those that land close to target, while avoiding the ones that had lower value by manipulating the postsaccadic reinforcement in the absence of a position error signal (Madelain, Paeye, & Wallman, 2011). In the present experiment the value of saccades is clearly related to the distance from the target and not to the distance from background features. Stated otherwise, saccades were reinforced by vision of the target, not by vision of the background. A similar conclusion was reached when using a postsaccadic target and distractor to probe adaptation (Madelain et al., 2010). The sensitivity of saccades to reinforcement is compatible with the observation that when monkeys had to perform a saccade in a direction associated with food, saccade peak velocities were higher, trajectories straighter and latencies shorter than in a nonreinforced direction (Lauwereyns, Watanabe, Coe, & Hikosaka, 2002; Takikawa, Kawagoe, Itoh, Nakahara, & Hikosaka, 2002; Watanabe, Lauwereyns, & Hikosaka, 2003). In humans reinforcement has been shown to affect several saccade properties (Madelain, Paeye & Darcheville, 2011) such as peak velocities and durations (Xu-Wilson, Zee, & Shadmehr, 2009), variability in saccade endpoints (Paeye & Madelain, 2011), saccade gain (Madelain, Paeye, & Wallman, 2011), or saccade latencies (Madelain, Champrenaut, & Chauvin, 2007). That saccade adaptation is selectively driven by the saccade

goal can be interpreted as further evidence of the saccadic system's sensitivity to reinforcement.

Conclusions

These experiments provide strong evidence that human saccade adaptation is well controlled by the postsaccadic target position and not by the displacement of a background image. This implies that the saccadic system is able to selectively use the post-saccadic visual signals originating from the target to control its gain while ignoring myriad signals related to the background. Our results also support a trans-saccadic comparison of features mechanism to drive adaptation, because we masked images during the saccade. Whether adaptation is controlled by a specific prediction error mechanism or by a general reinforcement process, these results strongly suggest that the saccadic system uses the movement goal for adapting to new sensorimotor contingencies.

Keywords: saccade adaptation, target selection, sensorimotor learning

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