

Saccade adaptation is unhampered by distractors

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Saccade adaptation has been extensively studied using a paradigm in which a target is displaced during the saccade, inducing an adjustment in saccade amplitude or direction. These changes in saccade amplitude are widely considered to be controlled by the post-saccadic position of the target relative to the fovea. However, because such experiments generally employ only a single target on an otherwise blank screen, the question remains whether the same adaptation could occur if both the target and a similar distractor were present when the saccade landed. To investigate this issue, three experiments were conducted, in which the post-saccadic locations of the target and distractor were varied. Results showed that decreased amplitude adaptation, increased amplitude adaptation, and recovery from adaptation were controlled by the post-saccadic position of the target rather than the distractor. These results imply that target selection is critical to saccade adaptation.

Keywords: saccade adaptation, target selection, sensorimotor learning

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Introduction

Saccades are the rapid movements of the eyes used to examine the environment, to read, and to react to the sudden movement or appearance of objects. Because they are so rapid—a 10 deg saccade lasts 40–50 ms in humans (Becker, 1989)—no useful feedback from the visual system can guide the course of each movement, since visual signals require 40–50 ms to reach the superior colliculus, the principal saccade-programming brain region (Goldberg & Wurtz, 1972; Li & Basso, 2008). Thus, saccades are often described as ballistic or open loop, in that the trajectory is programmed prior to the movement. Open-loop behaviors are kept accurate by parametric feedback, meaning that, although the ongoing behavior is not adjusted by feedback, the parameters of the control system governing the behavior can be adjusted by the consequences of the movement. In the case of saccades, much evidence shows that if the relation of the target and fovea is consistently changed the oculomotor system adjusts the amplitude or direction of saccades. When the origin of saccadic errors is weakness in the extraocular muscles caused by disease in humans (Kommerell, Olivier, & Theopold, 1976; Optican, Zee, & Chu, 1985) or by muscle surgery in monkeys (Optican & Robinson, 1980), the saccadic adjustment

constitutes oculomotor repair. More generally, this plasticity, called saccade adaptation, is a form of motor learning that continually maintains accuracy in response to new sensorimotor contingencies. In the laboratory, saccade adaptation is studied by experiments in which the target is surreptitiously moved while the eye is in flight and hence vision is impaired (McLaughlin, 1967). This intrasaccadic step paradigm can induce increases or decreases in saccade amplitude or changes in saccade direction. Saccade adaptation is usually viewed as being like a servo system in that the post-saccadic distance between fovea and target constitutes a “retinal error” signal, which induces a change in a system parameter (Noto & Robinson, 2001; Wallman & Fuchs, 1998; see Hopp & Fuchs, 2004, for a review). In most studies of saccade adaptation, the target is the only visual stimulus present, so there is no ambiguity about the response demanded by the oculomotor system. However, this simplified visual environment leaves an ambiguity about the nature of the error signal guiding saccade adaptation in the visually rich environment of daily life: Does any similar stimulus near the fovea after a saccade provide an effective error signal, or does only the target to which the saccade was directed suffice? To address this question, we have modified the conventional intrasaccadic step paradigm by introducing a new object—a similar distractor—during the saccade. If the target makes an

intrasaccadic step and the distractor is introduced at the former location of the target (Figure 1A, left panel), will the adaptation be less effective because there is also a stimulus near the fovea? If the target does not step back during the saccade, but a distractor appears at the back-stepped location (Figure 1A, right panel), will adaptation occur? Our results support the view that it is the target, not a distractor, that causes changes in saccade amplitude. This work has been presented in abstract form (Herman, Harwood, Wallman, & Madelain, 2010).

Methods

General methods

Three experiments tested whether adaptation could occur in the presence of two visual stimuli, a target and a distractor. Each trial started with a fixation period of 750–1,250 ms (Figure 1B) during which a target was displayed either 4, 5, 6, or 7 deg to the left of the center of the screen against a gray background (luminance 40 cd/m²). After this fixation period, the target stepped by 10 or 12 deg (each amplitude occurred with equal probability in a pseudorandom order) to the right and remained visible for 1,500 ms.

The target was either a green filled circle 0.5 deg in diameter or a 0.5 by 0.5 deg yellow filled square, with the distractor being the other stimulus. In all sessions, on every trial, one of the two stimuli was chosen to be the target with equal probability using a pseudorandom sequence. Therefore, we define the target as the object visible during the fixation period and the distractor as the object appearing at saccade onset. Subjects were instructed to first fixate the target and then make a saccade to the target as soon as they detected the step.

Experiment 1: Decreased gain adaptation

The first experiment tested whether decreased saccade amplitude would result from backward intrasaccadic steps of the target if a distractor were in the original target location, and whether having a distractor in the back-stepped location would cause decreased saccade amplitude if the target did not make an intrasaccadic step. Each subject experienced three experimental conditions in separate sessions. Each session was divided into three phases: 100 pre-adaptation trials (without distractor), in which the target was not stepped back at saccade onset, then 400 adaptation trials, in which either the target or the distractor (depending on the condition) was put in the back-stepped location during the saccade, followed by 150 recovery trials, in which the target did not step back after its original step.

The conditions differed in what occurred during the adaptation trials: In Intrasaccadic Step Plus Distractor trials, during the saccade the target stepped backward by 20% of the initial target step (2 deg and 2.4 deg for a 10 and 12 deg initial step, respectively), and at the same time, a distractor appeared at the position previously occupied by the target (Figures 1B, left and 1C, top row). During Single Step Plus Distractor trials, the target did not step back at saccade onset, but the distractor appeared left of the target (2 deg and 2.4 deg for a 10 and 12 deg initial target step, respectively; Figures 1B, right and 1C, bottom row). In Conventional Intrasaccadic Step trials, the target stepped backward by 20% during the saccade, with no distractor appearing.

Experiment 2: Increased gain adaptation

The second experiment tested whether forward intrasaccadic steps would increase saccade amplitudes in the presence of a target and distractor. The design was identical to the one used in Experiment 1 except that in the adaptation trials the target (or the distractor) reappeared during the saccade 2 degrees (or 2.4 deg for a 12 deg initial step) to the right of the initial position in order to induce an increase in gain (Figure 1C, middle panels).

Experiment 3: Recovery from decreased gain adaptation

In a third series of experiments, we asked whether the presence of the distractor would affect the recovery following decreased gain adaptation (Figure 1C, right). After 100 pre-adaptation trials, the saccadic amplitude was decreased by 200 Conventional Intrasaccadic Step trials (without a distractor), after which there were 200 trials in which either the target continued to step back during the saccade, but the distractor now appeared at the original target position (Intrasaccadic Step Plus Distractor trials, Figures 1B, left panel and 1C, top right) or the target remained in its original position and the distractor appeared in the back-stepped position (Single Step Plus Distractor trials, Figures 1B, right panel and 1C, bottom right). In a remaining 150 recovery trials, the distractor did not appear at saccade onset.

Participants

Five subjects each performed all of the experiments. Two were naive to the purpose of the experiments but had previous experience in oculomotor experiments; three were authors (subjects S3, S4, and S5). All had normal vision. The order of the eight experimental sessions (three in the first experiment, three in the second experiment, and two in

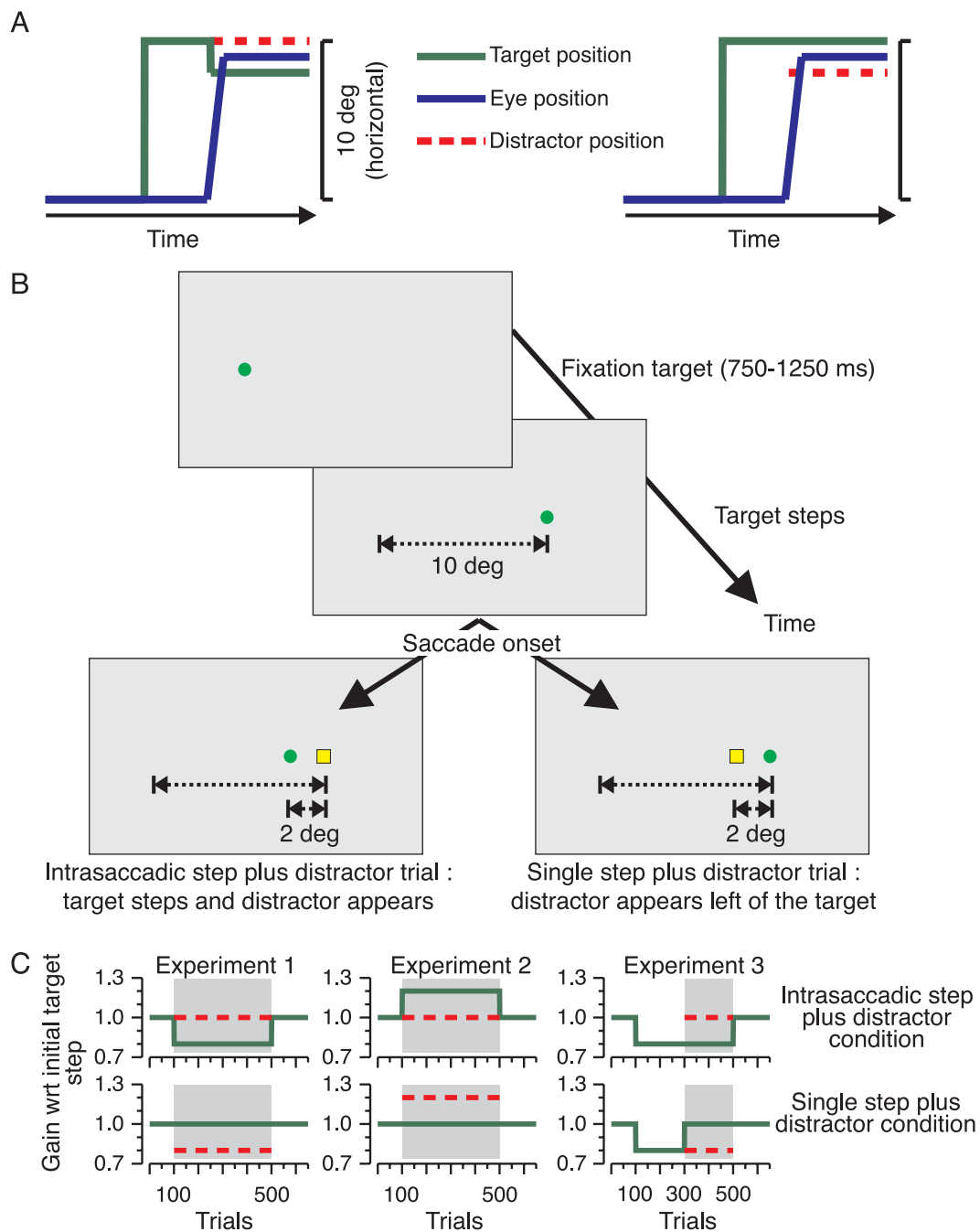


Figure 1. (A) Schematic diagram of the position errors following a 9 deg saccade for a 10 deg initial target step. In the Intrasaccadic Step Plus Distractor condition, in which the target steps back (left), the saccade (blue) would be hypermetric with respect to the target (green solid line) but hypometric with respect to the distractor (red dashed line). In the Single Step Plus Distractor condition, in which the distractor steps back (right), the reverse would be true. (B) Schematic diagram of the temporal sequence of trials used in each of these paradigms in Experiment 1. After a fixation period (750–1250 ms), the target (green disk) steps to the right. As soon as a saccade onset is detected, two stimulus configurations are possible, depending on the paradigm. In the Intrasaccadic Step Plus Distractor condition (left), the target (green disk) steps back by 20% of the initial target step while a distractor (yellow square) appears at the initial target location. In the Single Step Plus Distractor condition (right), the target position remains unchanged while a distractor appears left of the target. Note that although the square stimulus is shown with a black outline, the actual stimulus was all yellow (see [Methods](#) section). (C) Time course of the three experiments. All sessions began with 100 regular single step trials. In the Intrasaccadic Step Plus Distractor condition (upper graphs) or Single Step Plus Distractor condition (lower graphs) of Experiments 1 and 2, subjects experienced 400 adaptation trials (from trials 101 to 500) followed by 150 regular single step trials. In Experiment 3, the target–distractor arrangement of Experiment 1 was imposed only after 200 Conventional Intrasaccadic Step trials (that is, from trials 301 to 500), followed by 150 single step trials. Shaded areas indicate the adaptation phases, except in Experiment 3, in which it indicates the experimental recovery phase.

the third experiment) was randomized across subjects. Subjects usually performed one or two daily sessions.

Written consent was obtained from all subjects, and the experimental protocol was approved by the Institutional Review Board of the City College of New York.

Apparatus

Subjects in a darkened room viewed stimuli at a distance of 57 cm while on a bite board to minimize head movements. Stimuli were generated on a computer running VisionWorks (Vision Research Graphics, Durham, NH) and displayed on a 21-in. CRT display with a vertical refresh rate of 200 Hz. Pupil position was digitized at 240 Hz, using an infrared video eye-tracking system (ISCAN, Woburn, MA), controlled by a computer using the LabView software package (National Instruments). Immediately preceding each experimental session, a 50-point horizontal calibration was carried out by having the subject fixate a 0.3° target 10 times at each of five randomized horizontal screen locations while the experimenter pressed a key to acquire a 50-ms average of eye position. Locations were randomized to ensure that there was always a saccade between measurements. An online least-squares fit to these measurements was used, and the resulting slope and *y*-intercept were saved for calibration of the offline saccade measurements.

For online saccade detection, a real-time algorithm used a velocity criterion to identify the first saccade at least 100 ms after the target step. The change in visual display was triggered as soon as the velocity signal exceeded this fixed threshold.

Data analysis

All analyses were performed using MATLAB (The MathWorks, Natick, MA). During offline analysis, saccades were detected automatically using a velocity threshold of 10°/s and a minimum latency criterion of 100 ms to exclude anticipatory movements. The start and end of each saccade immediately following the target step were confirmed and, if necessary, corrected by the experimenter. Approximately 5% of all saccades were excluded from further analysis.

To describe the changes in amplitude, we computed the mean gain (and standard deviation) of the last 50 trials at each phase (pre-adaptation, adaptation, recovery) and compared the conditions using individual two-way ANOVAs (type of experiment: Conventional Intrasaccadic Step, Intrasaccadic Step Plus Distractor, Single Step Plus Distractor; phase: pre-adaptation, adaptation, recovery); post-hoc pair-wise *t*-tests were then computed using the Sidak correction. To show the trends of the adaptation and recovery within individual experiments, we smoothed the

records of saccadic gain vs. trial number by means of a Lowess iterative non-linear regression (span = 50 trials), separately for each phase of the experiment.

Results

Our results show that saccade gain (gain = saccade amplitude/target step amplitude) changes according to the target position and ignores the distractor: in all experiments, saccade adaptation occurred only in the Intra-saccadic Step Plus Distractor condition but not in the Single Step Plus Distractor condition. Moreover, the amount of adaptation observed with Intra-saccadic Step Plus Distractor trials was similar to what was obtained in the Conventional Intra-saccadic Step trials indicating that the saccadic system is able to selectively adapt its gain by following the position error associated with the target.

Experiment 1: Decreased gain adaptation

This experiment compared the decrease in saccadic amplitude after either the target or distractor stepped back by 20% of the initial target step. The results for each subject and the averages across subjects are shown in [Figure 2](#). Across subjects, the gain remained mostly unchanged in the pre-adaptation trials (trials 1–100). During the Intra-saccadic Step Plus Distractor adaptation trials, the gain quickly decreased (red dots) and then increased during the recovery trials, much as occurred with the Conventional Intra-saccadic Step condition (blue dots). In contrast, in the Single Step Plus Distractor condition (green dots), the gain remained mostly unchanged during the adaptation phase, with individual subjects showing little (S5, [Figure 2E](#)) or no change.

To evaluate the reliability of the changes in saccadic gain, we compared the gains obtained in the last 50 trials of the pre-adaptation, adaptation, and recovery phases for each condition using individual two-way ANOVAs (2, 2) and post-hoc all pair-wise *t*-tests using the Sidak corrections. In all subjects, we found a significant ($p < 0.05$) effect both of phase and of condition, as well as a significant interaction between the two factors. [Figure 2F](#) plots the means and standard deviations as well as the results of the corrected *t*-tests comparing the experimental trials in each condition. A blue star indicates a significant (corrected $p < 0.05$) difference between the Intra-saccadic Step Plus Distractor and the Conventional Intra-saccadic Step trials, while a green star indicates a significant difference between the Intra-saccadic Step Plus Distractor and the Single Step Plus Distractor trials. It can be seen that the gain was systematically and significantly lower during adaptation in the Intra-saccadic Step Plus Distractor

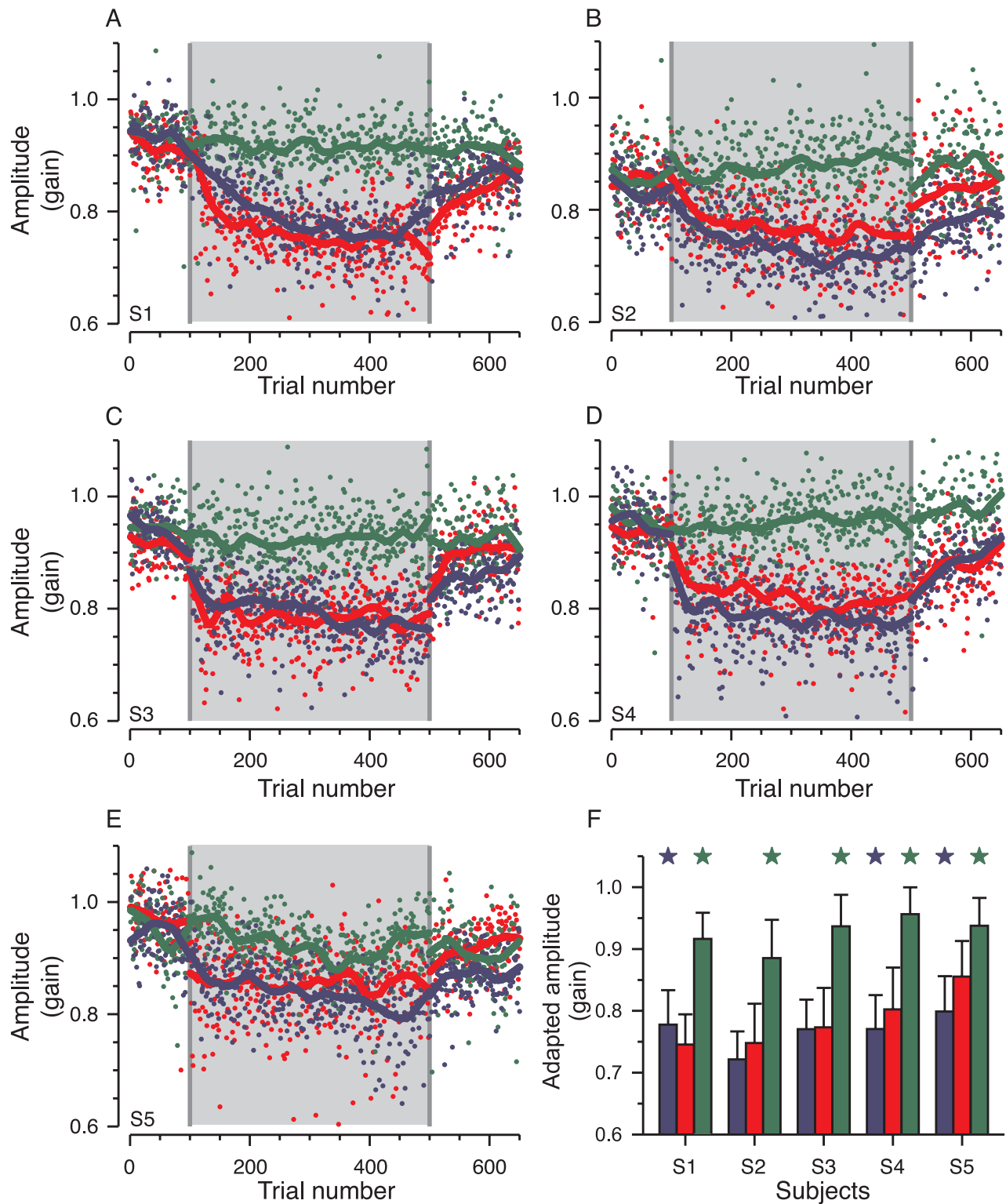


Figure 2. Decreased gain adaptation (Experiment 1). (A–E) Individual saccade amplitudes (expressed as gain) for all trials (subjects 1–5, respectively). Blue dots, Conventional Intrasaccadic Step condition; red dots, Intrasaccadic Step Plus Distractor condition; green dots, Single Step Plus Distractor condition. Solid lines, corresponding saccadic gain fit by Lowess smoother. Shaded areas indicate the adaptation phases. (F) Individual mean gains for the last 50 adaptation trials in the Conventional Intrasaccadic Step (blue), Intrasaccadic Step Plus Distractor (red), and Single Step Plus Distractor (green) conditions. Stars indicate statistically significant differences (corrected pair-wise t -tests $p < 0.05$) between the mean gain in adaptation phase in the Conventional Intrasaccadic Step trials versus the Intrasaccadic Step Plus Distractor trials (blue stars) and the Intrasaccadic Step Plus Distractor trials versus the Single Step Plus Distractor trials (green stars).

trials than in the Single Step Plus Distractor trials. This was not true when comparing the Conventional and Intrasaccadic Step Plus Distractor trials (gain: 0.77 and 0.78, respectively, when averaged across subjects): the gain was significantly higher in the Conventional condition for two subjects but significantly lower in one subject and unchanged in the other two subjects. It is perhaps noteworthy that, by the end of the adaptation phase, saccades once again tended to be hypometric with respect to the final target position.

Averaged across subjects, the same patterns were present: (a) As expected, there were no consistent differences among the conditions in the baseline trials. (b) There was a significant reduction in gain from the baseline to the adaptation phase with Intrasaccadic Step Plus Distractor trials (from 0.91 to 0.78), which was much like the reduction resulting from Conventional Intrasaccadic Step trials (from 0.91 to 0.77). (c) In contrast, there were no differences during the Single Step Plus Distractor trials (0.92 and 0.93). This pattern of results implies that subjects adapted equally well during both the Conventional and Intrasaccadic Step Plus Distractor trials but did not adapt during the Single Step Plus Distractor trials, showing that the target controlled changes in saccadic gain.

To evaluate whether the saccades themselves differ between the Intrasaccadic Step Plus Distractor trials and the Single Step Plus Distractor trials, we also compared the dynamics of saccades using the following equation (Lebedev, Van Gelder, & Tsui, 1996):

$$a = \frac{\text{PeakVelocity}}{\sqrt{\text{MovementAmplitude}}}. \quad (1)$$

The parameter a , which is directly proportional to peak velocity, was not significantly different in the two adaptation trial types (103 vs. 104.6 on average, paired t -test $p = 0.35$). Finally, the latencies of saccades adapted by either paradigm were also quite similar (216 vs. 210 ms on average, paired t -test $p = 0.49$).

Experiment 2: Increased gain adaptation

This experiment compared the increase in saccadic amplitude after either the target or distractor stepped forward by 20% of the initial target step (Figure 1C). The results for each subject and the averages across subjects are shown in Figure 3. In the pre-adaptation phase, the gain remained mostly unchanged, but in the adaptation phase, during the Intrasaccadic Step Plus Distractor trials (red dots), the gain for each subject (except subject 5, Figure 3E) increased and then decreased back toward normal during the recovery phase. The pattern of changes in gain was very similar in the Conventional Intrasaccadic Step trials (blue dots). In the Single Step Plus Distractor trials (green dots), the gain remained mostly unchanged.

In each subject, we found a significant (ANOVA (2,2), all $p < 0.05$) effect both of phase and of condition, as well as a significant interaction between the two factors, except for subject 5, in whom there was no significant effect of phase (Figure 3F). Every subject had significantly greater saccade amplitudes during adaptation with Intrasaccadic Step Plus Distractor trials than with Single Step Plus Distractor trials. Furthermore, in 4 of the 5 subjects, there was no difference between the Intrasaccadic Step Plus Distractor trials and the Conventional adaptation trials.

It can be seen that the gain was systematically and significantly higher during adaptation with the Intrasaccadic Step Plus Distractor trials than with the Single Step Plus Distractor trials (0.99 and 0.93, respectively, when averaged across subjects). This was not true when comparing the Conventional and Intrasaccadic Step Plus Distractor trials (gain: 1.01 and 0.99, respectively, when averaged across subjects): the gain was not significantly different in the Conventional trials for four subjects but significantly higher in subject 5.

Across subjects, we found a significant increase in gain from the baseline to the adaptation phase with Conventional Intrasaccadic Step trials (from 0.92 to 1.01) and with Intrasaccadic Step Plus Distractor trials (from 0.92 to 0.99), except again for subject 5 who did not significantly adapt during either the Conventional or the Intrasaccadic Step Plus Distractor trials. We did not find significant increases during Single Step Plus Distractor trials (from 0.92 to 0.93), except for subject 2 (from 0.84 to 0.88). This pattern of results confirms those results from Experiment 1 in that most subjects were able to selectively follow the relevant position error to control changes in saccadic gain.

Finally, we did not find significant changes in parameter a (107.3 vs. 103.6 on average, paired t -test $p = 0.07$) nor in the saccade latencies (225 vs. 185 ms on average, paired t -test $p = 0.25$).

Experiment 3: Recovery from decreased gain adaptation

The goal of this experiment was to probe the ability to recover from adaptation when the retinal error of the distractor encouraged a lower gain while the retinal error of the target encouraged a gain close to unity (Single Step Plus Distractor, Figure 1C, bottom right panel). To do this, the saccadic amplitude was first reduced in an adaptation phase of 200 Conventional Intrasaccadic step trials, followed by an experimental recovery phase of 200 trials in which either the distractor was introduced at the non-back-stepped location as in Experiment 1 (Intrasaccadic Step Plus Distractor) or the target stopped stepping back and the distractor was introduced at the back-stepped location (Single Step Plus Distractor). Given the results from Experiments 1 and 2, it is not surprising that the gain increased (i.e., recovered) when the target no longer stepped back.

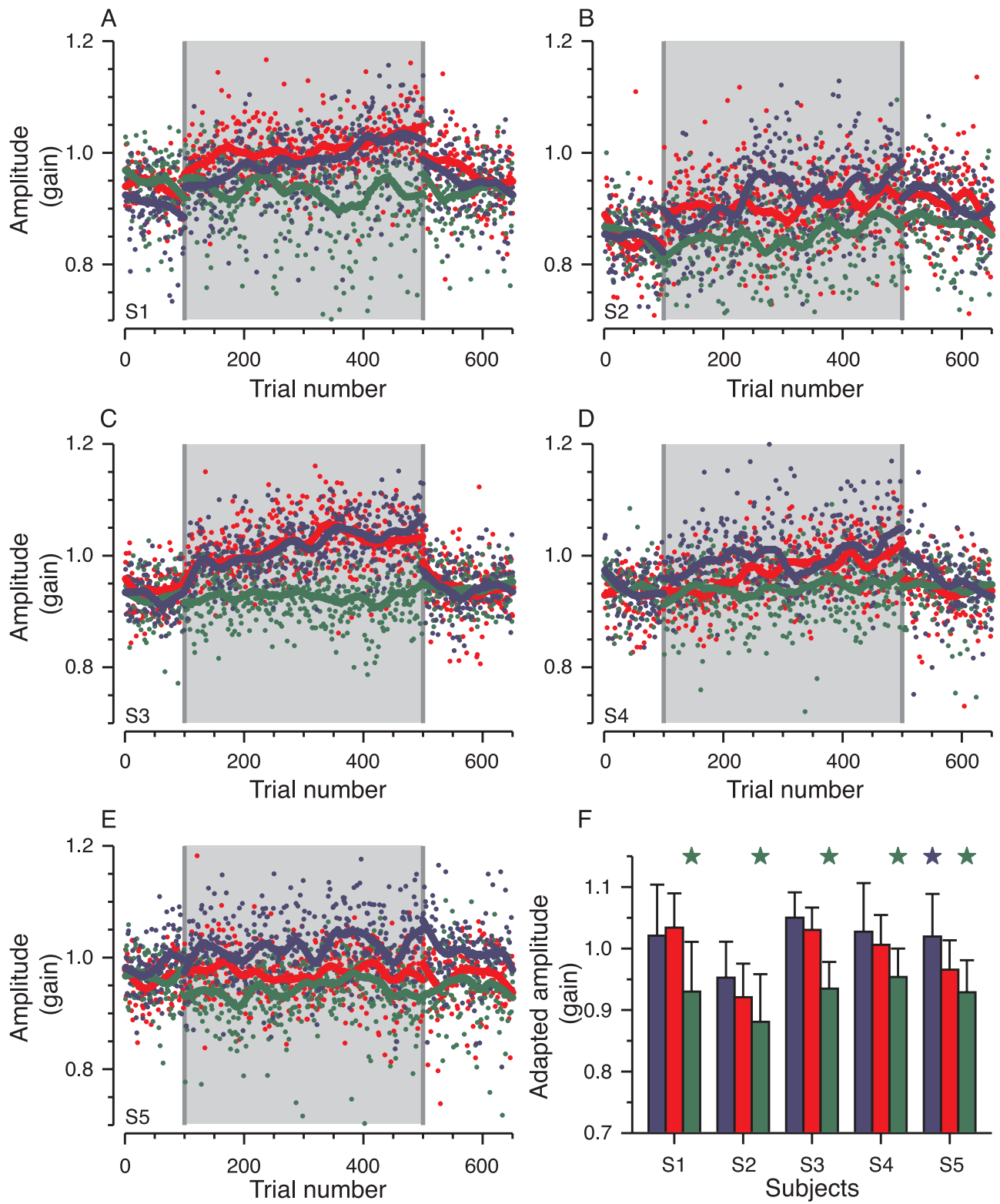


Figure 3. Increased gain adaptation (Experiment 2). (A–E) Individual saccade amplitudes for all trials (subjects 1–5). (F) Individual mean gains for the last 50 adaptation trials. Symbols and colors as in Figure 2.

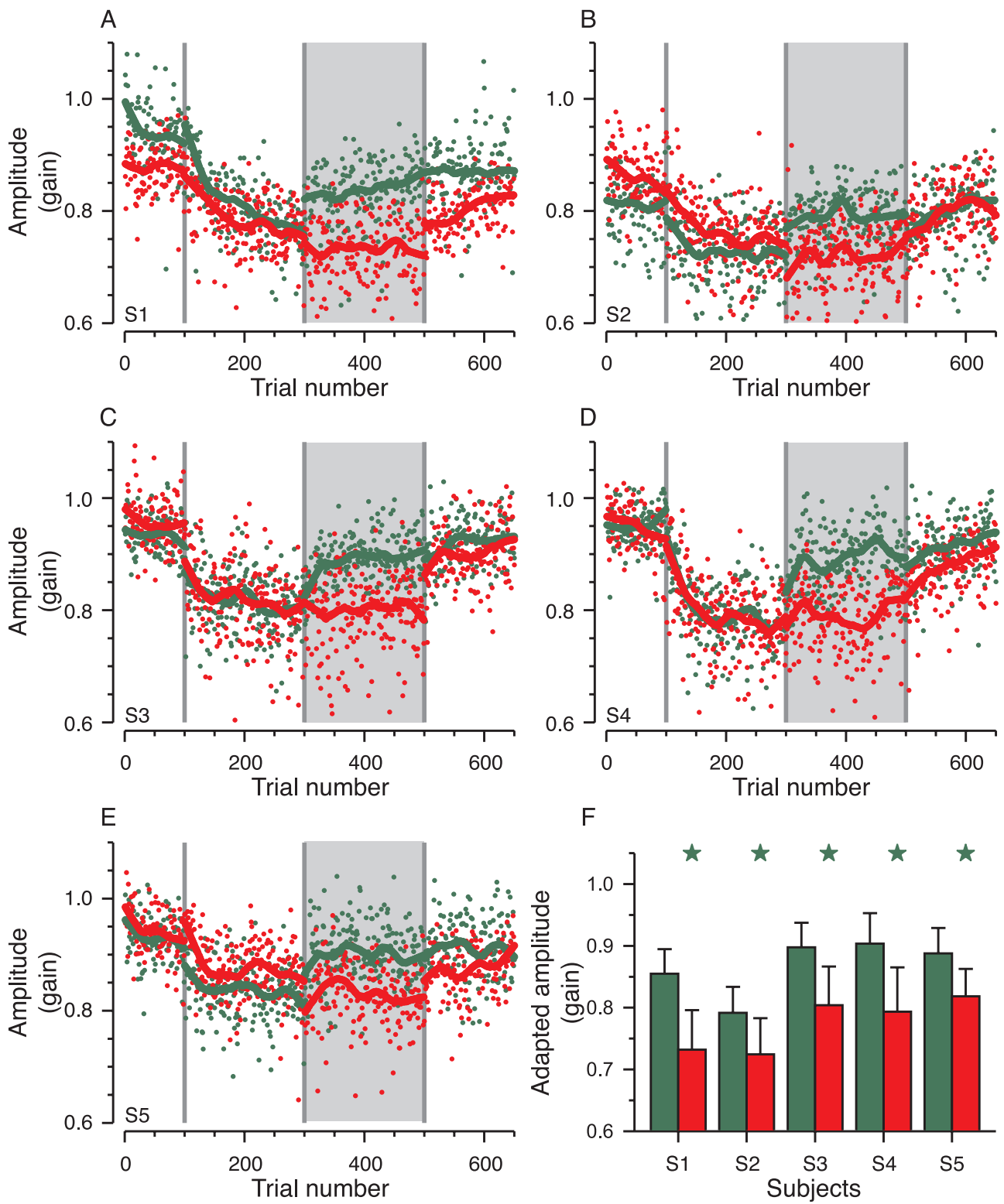


Figure 4. Recovery from decreased gain adaptation (Experiment 3). (A–E) Individual saccade amplitudes for all trials (subjects 1–5). Shaded areas indicate when distractor is present. (F) Individual mean gains for the last 50 experimental recovery trials. Symbols and colors as in Figure 2.

Figure 4 plots the saccadic gains for each trial for each subject. Across conditions, the gain remained mostly unchanged in the pre-adaptation phase and decreased in the Conventional adaptation phase. During the experimental recovery phase with Intrasaccadic Step Plus Distractor trials (red dots), the gain remained low (shaded epoch in **Figure 4**) and increased during the last 150 regular trials. In contrast, the gain increased during the experimental recovery phase with Single Step Plus Distractor trials (green dots, shaded epoch in **Figure 4**).

In every subject, we found a significant (ANOVA (3,1), $p < 0.05$) effect both of the phase and of the condition, as well as a significant interaction between the two factors, except for subject 2 in whom there was no significant effect of condition (**Figure 4B**).

Across subjects, after an expected decrease in gain during the adaptation phases (from 0.91 to 0.78), in the experimental recovery phase we found a significant increase in amplitude during the Single Step Plus Distractor trials (from 0.78 to 0.87), revealing a recovery from adaptation despite the presence of a distractor at the back-stepped location. In contrast, during the Intrasaccadic Step Plus Distractor trials, the gain remained low in the experimental recovery phase (0.79 to 0.77), with the gain in individual subjects remaining either unchanged (S1, S3, and S4) or significantly decreasing (S2 and S5), indicating that no recovery occurred in this phase while the target continued to be stepped back, despite the addition of the distractor. Finally, we looked at the differences from the experimental recovery phase to the subsequent trials without distractors. Because no recovery had occurred during the Intrasaccadic Step Plus Distractor trials, it is to be expected that there was a systematic and significant increase in gain in all subjects when the intrasaccadic steps ceased (**Figure 4**, red curves, from 0.77 to 0.87 averaged across subjects). In contrast, because the gain recovered nearly completely during the experimental recovery phase with the Single Step Plus Distractor trials (the gain only changed from 0.87 to 0.89 when averaged across subjects; **Figure 4**, green curves, shaded epochs), we found no significant additional recovery over the final block of trials without intrasaccadic steps in three subjects and a significant additional gain increase in two (S3 and S5).

As in Experiments 1 and 2, we did not find significant changes in saccade latencies between the two paradigms (209 vs. 182 ms on average, paired t -test $p = 0.28$). However, parameter a was slightly higher in the Intrasaccadic Step Plus Distractor trials (105.6 vs. 101.8 on average, paired t -test $p = 0.003$).

Discussion

Our results show that, in the presence of two conflicting post-saccadic visual stimuli, a target and a distractor, the

saccadic system selectively adapts its gain as though only the target were present.

In the first experiment, we observed the expected decreased gain adaptation when the target made a backward intrasaccadic step (without distractor). When a distractor was added at the original target location, at the same time as the target stepped backward (Intrasaccadic Step Plus Distractor condition, **Figure 1B**), we found that subjects essentially ignored the distractor and adapted to an extent comparable to the adaptation driven by the Conventional Intrasaccadic Step trials. In contrast, when the locations of the target and distractor were reversed, so that the distractor was at the back-stepped location and the target did not make an intrasaccadic step (the Single Step Plus Distractor condition, **Figure 1B**), adaptation did not occur. The degree of adaptation we observed in the Intrasaccadic Step Plus Distractor trials (14% decrease on average) was comparable to the change observed in Conventional Intrasaccadic Step trials (15% decrease on average), resulting in comparable final gains (0.78 and 0.77, respectively). By comparison, the final gain in the Single Step Plus Distractor trials was 0.93, i.e., a +1% increase when compared to the pre-adaptation phase. It has been previously reported that the amount of adaptation is usually less than the size of the adaptation step—in our case, -14% and -15% for a -20% step (Miller, Anstis, & Templeton, 1981; Robinson, Noto, & Bevans, 2003; Semmlow, Gauthier, & Vercher, 1987). Subjects were variable both in their pre-adaptation and adapted gains (compare **Figures 2A–2E**). Such inter-subject and inter-session variability has previously been observed in conventional adaptation (Erkelens & Hulleman, 1993).

Similarly, in the second experiment, in which the target was stepped forward (**Figure 1C**, middle panels), we found a significant gain increase during Conventional Intrasaccadic Step and Intrasaccadic Step Plus Distractor trials but not during Single Step Plus Distractor trials. However, the extent of adaptation in the Intrasaccadic Step Plus Distractor condition was only +8%, almost half of what was observed in the first (gain decrease) experiment. This asymmetry is also a prominent feature of conventional saccade adaptation; in our Conventional Intrasaccadic Step conditions, the average gain changed by +11% after forward-step trials, but -15% after back-step trials, although the target stepped by 20% for 400 trials in both cases.

The origin of this asymmetry between increased gain and decreased gain adaptations is unknown, and it may be related to saccades being naturally hypometric (Henson, 1978; Straube, Fuchs, Usher, & Robinson, 1997), perhaps because of a tonic tendency for the gain to decrease. It has also been suggested that distinct mechanisms are involved: a reduction of motoric gain in the case of decreased gain adaptation and a remapping of the desired goal for saccades in the case of increased gain adaptation (Ethier, Zee, & Shadmehr, 2008; Panouillères et al., 2009; Semmlow, Gauthier, & Vercher, 1989). It has been proposed that

recovery following an amplitude decrease adaptation may be the same as an increased amplitude adaptation (Deubel, Wolf, & Hauske, 1986). This might explain why the saccade amplitudes did not quite return to the pre-adaptation levels in either the Conventional Intrasaccadic Step adaptation experiments (0.86 vs. 0.91) or in the target plus distractor experiments (0.87 vs. 0.91).

In the third experiment, the saccade amplitude was first reduced with Conventional Intrasaccadic Step trials, and then the distractor was substituted for the target in the back-stepped location, while the target did not back step. In this case, the saccade amplitude returned toward the original unadapted amplitude, as though the distractor were not present. In contrast, if the target continued to step back, with the distractor added in the original target location, the saccade amplitude did not return toward the unadapted state. This experiment demonstrates that saccadic amplitude can increase toward its initial value when the target does not back step, even with a distractor at the back-stepped location (Figure 1C, right panels): gain increased by +12% in the target recovery condition versus –2% in the distractor recovery condition (Figure 4F).

Taken together, the results from the three experiments show that both adaptation and recovery are not impaired by the presence of a distractor. Because the target in our paradigms was defined trial by trial as the object present during the fixation period, not by its specific visual characteristics, we contend that only a mechanism of target selection can explain the present results. We will discuss, first, the general implications for understanding saccade adaptation and then the possible mechanism underlying this ability to select a particular error signal.

Target selection and saccade adaptation

Our results show that the mechanism of saccade adaptation is not blind to the identity of the target; instead, it must employ some process of target selection. We regard our experiment as a highly simplified version of the problem faced by the saccadic system in everyday life: For saccade adaptation to be driven by post-saccadic visual signals, the oculomotor system would need to know which of the myriad stimuli had been the target of the preceding saccade.

Because in our experiments the identity of the target and distractor changed from trial to trial, our finding that adaptation was driven only by the target suggests that a memory of the target is retained across saccades. In our experiments, we can envision the trans-saccadic memory as occurring at one or more of these levels: First, there may be a low-level automatic process that computes a cross-correlation between the scene around the target before and after the saccade and thereby redirects gaze to the target. Deubel (1991) has reported that when a saccade to a point on a one-dimensional random grating causes the grating to shift, adaptation occurs, despite the target not being

consciously identifiable. Second, the pre-saccadic process of target selection could result in an automatic storage of target identity in working memory, which could be read out post-saccadically. Although working memory is probably an intrinsic component of target selection and of attention, recent experiments have shown that task-irrelevant items in working memory can misdirect saccades to locations other than the target (Mannan, Pambakian, & Kennard, 2010; Soto, Hodsoll, Rotshtein, & Humphreys, 2008). Thus, having the target in working memory might explain our results without necessarily involving any other aspects of target selection. Third, and in our view, most importantly, the object being attended before the saccade may be automatically retained by attention across the saccade, and the distance of the fovea from the locus of attention may be an error signal driving saccade adaptation. We will discuss this possibility in the following section.

Ours is not the first experiment to show a role of some form of target selection in saccade adaptation. Ditterich, Eggert, and Straube (2000) showed that adaptation to the intrasaccadic stepping of a ring target on a busy background was impaired if the elements within the ring did not move with the ring, implying that the identity of the target influenced adaptation. Furthermore, a back step during a saccade to a target stepping from within one object to another causes more adaptation than the same target step and back step within an object (Collins, Vergilino-Perez, Beauvillain, & Dore-Mazars, 2007). Interestingly, even that paradigm of low-level adaptation—the VOR—also shows an influence of target selection (Eggers, De Pennington, Walker, Shelhamer, & Zee, 2003).

Attention and saccade adaptation

The fact that attention is drawn to the target location before every saccade (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Doshier, & Blaser, 1995) makes it a natural candidate for mediating trans-saccadic identification. The issue remains, is it object attention or spatial attention that is involved?

If object attention is involved, everyday experience suggests that when we attend to an object at a particular location, this attention is not disrupted by eye movements. Because the physiological substrate of attention presumably involves some activation of part of a retinotopic map, saccades would displace this retinotopic location dragging attention away from its target. Golomb, Chun, and Mazer (2008) have shown that, after a saccade, some attentional resources remain at the pre-saccadic retinal location, now displaced, but attention quickly returns to the spatial location of the previously attended object. The most parsimonious explanation of this finding is that a low-level mechanism uses either an efference copy or a proprioceptive signal to compensate for the saccadic displacement. The perisaccadic remapping of receptive fields observed in

neurons in the parietal cortex and elsewhere (Duhamel, Colby, & Goldberg, 1992) may be a manifestation of this process (Cavanagh, Hunt, Afraz, & Rolfs, 2010). Thus, in our experiments, the pre-saccadic allocation of object-based attention to the target would be retained after the saccade, and the distance of the fovea from this attentional focus might drive saccade adaptation.

Alternatively, it might be the case in our experiments that object-based attention is required only early in the adaptation phase. Subsequently, subjects might rely on the consistent post-saccadic presentation of the target in one location (relative to its pre-saccadic location) to pre-allocate attention to the back-stepped location. Once this occurs, this pre-allocated post-saccadic attention might either drive adaptation directly or might diminish the efficacy of stimuli elsewhere. If this were the case, it would not matter how much time after each saccade is required to relocate the target, given that postponing the post-saccadic presentation of a target reduces adaptation (Fujita, Amagai, Minakawa, & Aoki, 2002; Shafer, Noto, & Fuchs, 2000).

A priori, one might be skeptical of an attentional explanation because, in our experimental situation unlike real life, the distractor appears suddenly and might be expected to attract more attention than the target. However, changes occurring during saccades are generally not noticed except at the saccade target (Deubel, Schneider, & Bridgeman, 2002; McConkie & Currie, 1996). Because our distractors did not hamper saccade adaptation, we presume that the attention at the target before the saccade remained with the target after the saccade, rather than being drawn to the distractor.

Alternatives to retinal error as the signal guiding adaptation

In the laboratory, oculomotor adaptation is conventionally studied by having subjects make saccades to a simple spot target on an otherwise blank screen, so that after the target is displaced during the saccade, the eye is further from the target than it normally would be. This visual error signal (“retinal error”) is widely considered to be the error signal that guides the adjustment of saccade amplitudes over many trials (Noto & Robinson, 2001; Wallman & Fuchs, 1998). The evidence of target selection being involved in saccade adaptation is only one of the reasons for questioning the primacy of this error signal as guiding saccade adaptation. Another reason is the evidence that adaptation can be driven by consistent post-saccadic deviations from the predicted target location, even if these are at odds with the retinal error. For example, by instructing subjects to make saccades two-thirds of the way to the target and then back stepping the target a little during saccades, Bahcall and Kowler (2000) observed a decrease in saccadic gain even though the target was beyond the fovea after the saccade. More recently, Wong and Shelhamer (2009) showed that, by taking advantage of

the tendency of normal saccades to be hypometric, the target could be placed so that after the saccade the target was generally stepped back by such a small amount that it remained beyond the fovea, and yet saccade amplitude was adapted downward. This result could be interpreted as a manifestation of the mechanism that maintains the hypometricity of the saccades, much like the findings of Henson (1978) and Robinson et al. (2003) that placing the target on the fovea results in decreased saccade amplitude. This sensitivity of saccade adaptation to deviations from predicted outcomes has been formalized in the models in which a forward controller compares the expected visual error with the computed position during the saccade and adjusts the saccade trajectory accordingly, constituting the quick acting component of saccade adaptation (Chen-Harris, Joiner, Ethier, Zee, & Shadmehr, 2008; Davidson & Wolpert, 2005). These models are related to the visual comparison models in which adaptation depends on a comparison of the retinal image after the saccade lands with the image that would be predicted based on the size and direction of the planned saccade (Bahcall & Kowler, 2000; Ditterich et al., 2000). Thus, motor learning would consist of learning to predict the consequences of an action.

A final argument against retinal error being the only error signal guiding saccade adaptation is the finding that saccades of a single direction and amplitude can have two different adaptation states depending on context. This has been shown both with a proprioceptive context (Alahyane & Pelisson, 2004; Shelhamer & Clendaniel, 2002) and with a visual context (Herman, Harwood, & Wallman, 2009). This contextual adaptation may also explain why there is some maintenance of adaptation after 24 h in monkeys (Noto, Watanabe, & Fuchs, 1999) and after several days in humans (Alahyane & Pelisson, 2005), despite thousands of unperturbed saccades made between sessions.

Whatever the hierarchy of error signals guiding adaptation, because the normal variability of saccade landing positions causes some saccades to land closer to the target and others closer to the distractor, one can hypothesize that those landing near the target have greater “value” than those landing near the distractor. If the saccades of greater value were more likely to be repeated because of this reinforcement, this could explain the target-oriented adaptation we observed. The sensitivity of saccades to “value” is compatible with the findings that in monkeys saccades to rewarded locations had shorter latencies (Ikeda & Hikosaka, 2003; Lauwereyns, Watanabe, Coe, & Hikosaka, 2002; Watanabe, Lauwereyns, & Hikosaka, 2003) and higher peak velocities than saccades of the same amplitude to non-rewarded locations (Takikawa, Kawagoe, Itoh, Nakahara, & Hikosaka, 2002). In humans, it has also been shown that saccadic peak velocities increased when viewing the visual stimulus was rewarding (Xu-Wilson, Zee, & Shadmehr, 2009), and we have found that saccadic latencies can be altered by reinforcement (Madelain, Champrenaut, & Chauvin, 2007) and that saccadic amplitude can be controlled by reinforcement contingencies in

the absence of a position error signal (Madelain, Paeye, & Wallman, 2008). Distinguishing effects of reinforcement from effects of attention is difficult (Maunsell, 2004), in part because the manipulation of reward is commonly used to control attention.

Conclusions

These experiments provide strong evidence that saccade adaptation can occur in the presence of two competing retinal errors, implying that the saccadic system is able to selectively use the signal originating from the target to change its gain, while ignoring the one related to a distractor. Whether saccade adaptation is guided by a servo system, using a variety of error signals, or by reinforcement, the existence of a role for target selection opens new doors to understanding the underlying mechanisms.

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