Temporal Characteristics of Error Signals Driving Saccadic Gain Adaptation in the Macaque Monkey

JENNIFER L. SHAFER, CHRISTOPHER T. NOTO, AND ALBERT F. FUCHS

Regional Primate Research Center and Department of Physiology and Biophysics, University of Washington, Seattle, Washington 98195

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Saccadic gain (saccade amplitude/target amplitude) can be reduced gradually by repeatedly stepping the target backward during the saccade. The gain reduction produced by this paradigm is thought to be driven by an error signal created by the backstep. We investigated the effects of varying the timing of this error signal relative to the end of the saccade by using two different paradigms in macaques. In the brief backstep paradigm, the target was stepped backward 30% during the saccade but extinguished after different durations. For very short backstep durations (32 ms), little gain reduction occurred. As backstep duration increased, the amount of gain reduction also increased. When backstep duration reached 80 ms, the amount of gain reduction was just under that achieved during the conventional adaptation paradigm in which the backstep remained visible for 1000–1200 ms. In the delayed backstep paradigm, as the saccade occurred, we extinguished the target and then, after a delay, illuminated it for 1 s at the backstep location. In most experiments with short delay times of 16–64 ms, the saccadic gain reduction reached that achieved during conventional adaptation. At delays of 112–208 ms, the amount of gain reduction decreased to ~75% of that reached during conventional adaptation. With still longer delays, the amount of gain reduction decreased more gradually. At delays of 750 ms, average gain reduction was 10%. By delays of 1.5 s, gain reduction had fallen essentially to zero. Taken together, these data suggest that the error signal must be present for a limited time (~80–100 ms) after the saccade to produce the most robust saccadic gain adaptation. However, errors present as long as 750 ms after the saccade still can produce a significant gain reduction.

INTRODUCTION

Saccades aim the line of sight at objects of interest. In the laboratory, we elicit saccades by rewarding primates for following jumping target spots with their eyes. The relation between the size of the saccade and the target jump that elicits it can be altered by causing the target to jump backward toward the initial fixation point during a targeting saccade (McLaughlin 1967). If this paradigm is continued for ~100 saccades in humans and ~1000 saccades in monkeys, saccadic gain, the ratio of saccade size to the size of the target step, will decrease (Albano and King 1989; Deubel 1987; Deubel et al. 1986; Miller et al. 1981; Semmlow et al. 1989; Straube et al. 1997). This saccadic adaptation does not simply reflect a distortion in the neural map of the visual world; rather it results from an alteration in the motor control of the saccadic response (Wallman and Fuchs 1998).

The signal that drives the motor adaptation appears to be visual, i.e., the error between eye position at the end of an errant saccade and the location of the target. This conclusion is based on experiments in which the target was stepped back briefly after the saccade and then returned to the initial target displacement. The duration of the backstep was adjusted to be so brief (~120–280 ms) that corrective saccades seldom occurred (Wallman and Fuchs 1998). Nevertheless, a substantial amount of gain reduction still was produced (~50% of that obtained by conventional saccadic adaptation). These data suggest that some component of the error signal is visual. However, because these brief backstep conditions, in which few if any appropriate corrective saccades occurred, did not produce full gain reduction, it is possible that a second component of the error signal is derived from the corrective saccades. This is a reasonable possibility because both the visual error and the corrective saccade that it elicits decrease as adaptation progresses. Alternatively, it is possible that the error signal is entirely visual but that the timing of the visual error signal in the experiments of Wallman and Fuchs (1998) was inappropriate to be maximally effective.

In the study described here, our objective was to explore more closely the postsaccadic interval during which an error signal can influence saccadic gain adaptation. We approached this interval from both ends by means of two different experiments. In the first, we stepped the target backward during a saccade and then extinguished it after different durations. In the second, we extinguished the target during a saccade and reilluminated it at a backstepped location after different time delays.

METHODS

Subjects and general procedures

Subjects were two juvenile rhesus macaques (Macaca mulatta), monkeys CR and SP. Eye movements were measured with an electromagnetic search coil technique with a sensitivity of 15 min of arc and a bandwidth of DC to 500 Hz (Fuchs and Robinson 1966; Robinson 1963). Coils were implanted on the sclera and under the...
conjunctiva of the left eye during aseptic surgery. At the same time, three lugs of dental acrylic were constructed over screws fastened to the skull so that we could immobilize the head during experimental sessions (Straube et al. 1997).

Both monkeys were trained to follow with their eyes when a target spot jumped horizontally. Whenever a monkey’s eye position remained within 2° of the target continuously for several seconds, with a grace period for the saccadic reaction time, it was rewarded with applesauce. After training, monkeys followed the target spot reliably for several thousand trials per day.

For all experiments, the monkeys sat in a chair in a darkened booth with their heads restrained from moving. Targets were projected onto either a screen or a drum 57 cm directly in front of the monkey. The target was a small red laser spot that subtended either a 0.25° on the screen or 0.4° on the drum. The laser beam was intercepted and deflected by two orthogonal mirrors mounted on galvanometers that were controlled by a Macintosh IIfx computer. In response to signals commanding target steps between 5° and 20°, the mirror settled to its new position within ~8 ms.

To assess the subject’s preadapted and postadapted gain, we collected at least 80 saccades to simple target steps both before and after each adaptation session. We then analyzed the first 20 saccades to each of four target steps: 10° and 13° leftward and 10° and 13° rightward; the same target amplitudes were used during adaptation. During the pre- and postadaptation blocks, the spot jumped by 10° or 13° either to the right or left within a maximum target excursion of ±20° of straight-ahead. The four target steps were selected pseudorandomly so that the monkey could guess neither the direction nor the size of the next target movement.

All surgeries and training procedures were approved by the Animal Care and Use Committee at the University of Washington. The animals were cared for by the veterinary staff of the Regional Primate Research Center. They were housed under conditions that comply with the National Institute of Health standards as stated in the Guide for the Care and Use of Laboratory Animals and with recommendations from the Institution of Laboratory Resources and the American Association for Accreditation of Laboratory Care International.

### Adaptation paradigms

#### CONVENTIONAL ADAPTATION

During conventional adaptation, the occurrence of a saccade to one of the four target steps was detected when horizontal eye velocity exceeded ~75°/s. When horizontal eye velocity decelerated to ~30°/s near the end of the saccade, the target spot was stepped backward toward its starting position by 30% of its initial jump, i.e., 3° for a 10° saccade and 3.9° for a 13° saccade. Because of the backstep, the monkey’s initial saccade landed past the target and then a corrective saccade was made to the backstepped target position. The target remained there for random times between 1000 and 1200 ms whereupon the next target step of either 10° or 13° was launched. Over time, the monkey’s first saccade gradually became smaller so that it eventually landed very near the final target; in many trials, no corrective saccade was needed. Previous studies have shown that this conventional adaptation reaches a nearly asymptotic gain after 600–2000 trials (Straube et al. 1997). To ensure adequate opportunity for adaptation to occur during our experiments, each adaptation session consisted of ~1700 trials (~850 in each direction).

#### BRIEF BACKSTEP ADAPTATION

To determine the minimum duration of the postsaccadic error that produced robust gain reduction, we varied the period of time that the backstepped target remained visible. In this paradigm, each trial began as in conventional adaptation. However, after the target spot had stepped backward by 30%, it remained visible for either 16, 32, 48, 64, 80, 112, 160, 208, or 304 ms before disappearing; only one backstep duration was used in each adaptation session. The spot reappeared 1000–1200 ms later and another trial began shortly thereafter at that target location. Monkey CR was not tested on the 16 and 160 ms backstep durations and monkey SP was not tested on the 48 and 208 ms durations.

#### DELAYED BACKSTEP ADAPTATION

To test the effect on adaptation of delaying the postsaccadic error, we varied the length of time between the subject’s saccade and the appearance of the backstepped target. The end of the subject’s saccade to the target spot was detected as before. However, in these experiments the spot was then extinguished for either 64, 112, 208, 512, 752, 1008, or 1504 ms; only one backstep delay was used in each adaptation session. After the delay, the spot appeared at the backstepped position and a corrective saccade moved the eye toward the target. Another 1000 to 1200 ms elapsed before the next trial commenced.

The end of the saccade was taken as the time at which horizontal eye velocity had fallen to ~30°/s. Because that time occurred an average of ~12 ms before the end of 85 randomly selected 10° and 13° saccades and because the mirror galvanometers that position the target settled within 8 ms or so, the backsteps in the brief backstep adaptations occurred ~4 ms before the end of the saccade. Similarly, the delay times were measured relative to the same time point nearly at the end of the saccade. In essence, therefore, the backstep durations and backstep delays reported in these experiments were measured relative to the end of the saccade. In both backstep paradigms, we ran at least two and as many as six adaptation sessions at each duration or delay. In each session, saccades of 10° and 13° in one or both directions were adapted and tested.

### Data processing and analysis

Data were collected with the use of customized hardware and programs on a Macintosh IIfx computer. Just before the computer sent the command to move the galvanometers and just after they had moved, the actual target position was sampled at 1 kHz. Target start and stop positions were determined from a three-point average before and after the target step. As the computer sent the command signal to move the target, horizontal eye position was sampled at 1 kHz for the next second. Instantaneous eye velocity was calculated from a five-sample moving boxcar average. When eye velocity exceeded 75°/s, a saccade was said to occur. The saccade was considered to be finished when its velocity fell to 30°/s and the eye position in the steady fixation period prior to the saccade. Target amplitude was taken as the difference between the eye position when eye velocity fell to 30°/s and the eye position in the steady fixation period prior to the saccade. Target positions before and after the movements, the calculated saccade (E) and target (T) amplitudes, and the horizontal saccadic gain (G = E/T) were exported to a spreadsheet. From these data we calculated the average percentage of change in gain for each single postadapted saccade as

\[
\text{Percentage of change} = \frac{\text{AVERAGE } G_{\text{PRE}} - \text{SINGLE } G_{\text{POST}}}{\text{AVERAGE } G_{\text{PRE}}} \times 100
\]

where AVERAGE G_{PRE} is the average preadapted gain for all (20) saccades to target steps of 10° or 13° to the right or left, and SINGLE G_{POST} is the gain for each of the 20 saccades measured after adaptation to the same four target steps. This strategy allowed us to calculate the percentage of change in gain for each saccade so that we could perform statistical tests on our results.

All statistical comparisons, except for those described in Figs. 2C and 5C, were based on t-tests between two samples assuming unequal variances. Differences between the means were taken as significant when P ≤ 0.05. In Figs. 2C and 5C, comparisons were performed with a one-way analysis of variance (ANOVA) using the Bonferroni/Dunn correction for repeated tests. Data from each experiment at each duration or delay was compared with data from each conventional adaptation on the same monkey. Each data set contained 20 individual values. Comparisons were taken as significant when P ≤ 0.05. Further details concerning comparisons for specific experiments are discussed in RESULTS.
RESULTS

Brief backstep

Figure 1 shows representative data obtained during brief backstep experiments on monkey CR. Each panel (A–D) shows data from eight different adaptation experiments: one experiment for each of seven backstep durations and one conventional adaptation (CA). In each backstep experiment, the target stepped backward for a different duration, ranging from 32 ms to 304 ms, and was then extinguished. The mean preadapted gain (calculated from open data points) varied from experiment to experiment; for example, in Fig. 1B it ranged from an average of 0.85 for the 48 ms adaptation session to an average of 0.98 for the conventional adaptation session. Because saccades normally are slightly hypometric (Becker 1989), preadaptation gains of <1.0 were not unexpected. In our experiments, slight hypometria also can be due to an animal’s experimental history. After a subject had undergone a gain reduction, a slight hypometria often persisted on the next day even though we had given the animal numerous ordinary target steps immediately after the gain reduction to promote gain recovery toward 1.0 (Noto et al. 1999).

For both monkeys, the amount of gain reduction depended on the length of time that the backstepped target remained visible. For the representative experiment in Fig. 1D, backstep durations of ≥80 ms produced postadaptation gains (filled circles) that were relatively constant and very similar to those produced by conventional adaptation (CA). For example, average postadaptation gains were 0.81, 0.80, 0.78, and 0.82 for durations of 80, 112, 208, and 304 ms, respectively, and 0.80 for conventional adaptation. For 32-ms backstep durations, there was no gain reduction at any of the four target amplitudes (average gain of 0.94 compared with 0.93 preadaptation). However, as backstep duration increased to 48 ms, there was a clear decrease in gain. For example, for 13° leftward target steps (Fig. 1D), average gain was 0.86. At 64 ms, the gain was about the same, i.e., 0.85. For most target steps (Fig. 1, B–D), the percentage of change in gain (see METHODS; Fig. 1, right ordinate) increased as the duration increased from 32 to 64 ms,
and then remained relatively constant for durations of >80 ms. For 10° rightward target steps (Fig. 1A), the percentage of change in gain reached a relatively constant value at somewhat greater durations of 112 ms.

For each of the four different target steps (left and right, 10° and 13°), the percentage of change in gain varied similarly with backstep duration across all experiments with each monkey. Therefore we averaged the percentage of change in gain for each type of target step separately at each duration.

The average percentage of gain reduction increased with backstep duration for both monkeys (Fig. 2, A and B). For monkey CR, the average gain changes for durations of 32, 48, and 64 ms were 3.9, 9.8, and 12.4%, respectively. For monkey SP, the average gain changes for durations of 32 and 64 ms were 11 and 13.8%, respectively, and 6.6% for durations of 16 ms. Monkey CR was not tested at a duration of 16 ms because ≥60% of experiments at 32 ms produced gain changes that were not significantly less than average preadaptation gains in this monkey (t-test, P > 0.05). For both monkeys, the average percentage of change in gain at durations of ≥80 ms was nearly constant. For monkey CR, the average percentages of change in gain for backstep durations of 80, 112, 208, and 304 ms were 15.2, 15.3, 14.8, and 15.3%, respectively (Fig. 2A). For monkey SP, the average percentages of change in gain for durations of 80, 112, and 304 ms were 16.5, 14.2, and 14.7%, respectively (Fig. 2B). For durations of ≥80 ms, both monkeys reached virtually the same average plateau, i.e., 15.0% for monkey SP and 15.1% for monkey CR.

The data in Fig. 2, A and B, show that the percentages of change in gain increased until they seemed to become quite similar to those produced by conventional adaptation (horizontal bar in CA column). To determine how similar they were, we separated all backstep adaptation data into sets according to the four target amplitudes (10° and 13°, left and right) and then compared them with each conventional adaptation set obtained for the same target amplitude. For example, at a backstep duration of 64 ms, monkey CR participated in five gain reduction sessions: two for leftward target steps only, one for rightward target steps only, and two for target steps in both directions. In each of the seven directions, two target amplitudes, 10° and 13°, were adapted for a total of 14 data sets. Monkey CR also participated in four conventional adaptation sessions with all four target amplitudes. Therefore at 64 ms in monkey CR, we made a total of 4 × 14, or 56, comparisons. Figure 2C illustrates the percentage of these comparisons in which the average percentage of change in gain was not significantly less than that produced by conventional adaptation (one-way ANOVA, P > 0.05). For example, at 64 ms for monkey CR, 63% results because the percentage of change in gain was not less than that after conventional adaptation in 35 of the 56 comparisons. For backstep durations of ≥80 ms, most experiments with both monkeys (~86% with monkey CR and ~62% with monkey SP) exhibited gain reductions that were not significantly less than the gain reduction produced by conventional adaptation. However, even for backstep durations of 304 ms, the percentages of gain reductions in some experiments, especially those with monkey SP, were significantly less than those produced by the 1000- to 1200-ms backsteps of conventional adaptation.

CORRECTIVE SACCADIES. As mentioned in the introduction, it is possible that the error signal driving adaptation not only has a visual component related to the error between eye and target position after the initial saccade, but also has a component derived from the corrective saccade that the postsaccadic visual error elicits. To explore whether changes in the characteristics of the corrective saccades reliably account for the differences in gain change associated with different backstep durations, we considered corrective saccades during some representative adaptions. In particular, we examined those that produced the data in Fig. 1D. We compared the characteristics of corrective saccades following short backstep durations where little gain reduction was produced (i.e., 48 ms, single open downward arrow) with those of corrective saccades following longer backstep durations that produced essentially conventional gain reduction (i.e., 112 and 304 ms, double open downward arrows). In all three experiments, we examined responses during
the first 140 trials of the adaptation paradigm. We considered the direction of corrective saccades, the interval from the end of the initial saccade to the corrective saccade, and the number of corrective saccades.

For backstep durations of 304 ms, corrective saccades were essentially horizontal (mean vertical component amplitude $= -0.02 \pm 1.3^\circ$) with magnitudes of <4° (Fig. 3A, white circles in shaded area). Most of these corrective saccades occurred at intervals between about 100 and 300 ms and therefore were launched when the backstepped target was still visible (Fig. 3B, white circles in shaded box).

For backstep durations of 112 ms, many corrective saccades were oblique. For example, some had a substantial downward vertical component of $2^\circ$ (see data cluster below shaded area in Fig. 3C). This downward component was probably the result of the upward drift that this monkey displayed in the dark between the time that the target disappeared after the 112 ms backstep until it reappeared ~1 s later. Indeed, most (87%) of the corrective saccades in this cluster occurred at intervals of >1100 ms, i.e., after the target had been turned back on (Fig. 3D). Therefore the corrective saccades elicited after 112-ms backsteps differed from those elicited after 304-ms backsteps in several ways: more tended to have vertical components and more had intervals >400 ms, which was the largest interval of the majority of responses in the 304-ms backstep condition (shaded bar). Nevertheless, the gain reduction in both conditions was the same (Fig. 1D, double arrows; t-test, $P > 0.5$).

For the shortest backstep durations of 48 ms, many of the corrective saccades had vertical components, most of which were upward and some of which were quite large (Fig. 3E). In these experiments, the backstep was extremely brief and the monkeys often looked away from the extinguished target in the 1-s interval before the target came back on. Sometimes these “corrective” movements were considerably slower than normal saccades and resembled drifts of the eye. In addition, almost all of the corrective saccades had intersaccadic intervals ≥200 ms, with many clustered between 200 and 400 ms (Fig. 3F). Consequently, both the direction and latency of the corrective saccades in the 48-ms backstep condition differed substantially from those in the 304-ms backstep condition. Also, the gain reduction in the 48-ms backstep condition (Fig. 1D, single arrow) was significantly less than that in the 304-ms backstep condition (Fig. 1D, double arrows; t-test, $P \leq 0.05$).

Finally, within the first 140 trials, all three backstep durations produced comparable numbers of corrective saccades.

**Delayed backstep**

Figure 4 shows representative data obtained during delayed backstep experiments on monkey CR. Each panel (A–D) shows data from eight different adaptation experiments: one experiment for each of seven backstep delays and one conventional adaptation (CA). In each experiment, the time delay between the end of the saccade and illumination of the target in a backstepped location was different, ranging from zero, which corresponds to conventional adaptation, to 1504 ms. Data from each of the four target steps associated with a specific delay were averaged separately for each experiment.
each step to find average gains for that condition. There was no apparent difference in the preadaptation gains with respect to the target amplitude or the specific backstep delay that was later adapted. The average preadaptation saccadic gain for all leftward target steps was 0.95, whereas that for all rightward target steps was 0.94.

For both monkeys, the postadaptation gain depended on the time delay between the saccade and illumination of the backstepped target. Postadaptation gains were lowest at zero delay (CA) and highest after the maximum delay of 1504 ms. For the representative data in Fig. 4B, average postadaptation gains for delays of 64 and 112 ms (0.76 and 0.77) were essentially the same as that for conventional adaptation (0.79). For delays between 112 and 200 ms, the postadaptation gain rose to 0.83. For even larger delays, the gain continued to increase, but more gradually, until it was only slightly less than normal for the maximum delay of 1504 ms. Similar trends can be observed in the data for the other three target conditions (Fig. 4, A, C, and D).

Pre- and postadaptation data were used to determine the percentage of change in gain separately for each target step (Fig. 4, dashed lines). For both monkeys, the gain data for the four target steps showed similar trends and therefore were combined (Fig. 5). For both subjects, the percentage of change in gain decreased as the backstep delay increased. For monkey CR (Fig. 5A), average percentages of gain decrease for delays of 0, 64, 112, 208, 512, 752, 1008, and 1504 ms were 15.8, 17.8, 16.5, 11.8, 8.3, 8.7, 6.1, and 5.9%, respectively. Between backstep delays of 112 and 208 ms, the percentage decreased rather steeply from 16.5% to 11.8%; the decrease was significant (t-test, _P_ < 0.05). For longer delays, the average gain decrease continued at a lesser rate until a delay of 1008 ms, after which it remained fairly constant. The percentage of change in gain for monkey SP followed this same general pattern although with different details (Fig. 5B). For the same backstep delays, this monkey’s average gain changes were 18.1, 16.5, 13.7, 13.5, 14.6, 11.4, 10.3, and 5.1%, respectively. The initial rapid decrease occurred between 80 and 112 ms and the subsequent gradual decrease in the percentage of change in gain continued until 1504 ms.

For each monkey, the data at each delay time again were separated according to the four target amplitudes, and separate comparisons were made with conventional adaptation data (as was done in Fig. 2C). Figure 5C shows the percentage of these comparisons in which the average percentage of change in gain was not significantly less than that produced by conventional
DISCUSSION

Our data illustrate that the amount of gain reduction produced by an intrasaccadic target jump depends on how long the displaced target is present after the saccade. The data from the two experiments presented here converge on the idea that the target motion within the 80–100 ms or so after the saccade is the most influential in determining the amount of adaptation that the backstepping target will produce. However, errors occurring up to 750 ms after the saccade still can influence gain reduction.

The period immediately after (within 80–100 ms) the saccade

In the experiments described here, the conventional adaptation paradigm, in which the target backstep remained continuously visible for 1000–1200 ms, produced an average gain reduction of 15.8% in monkey CR and 18.1% in monkey SP. Our brief backstep experiment showed that only when the displaced target remained visible for >80 ms did a nearly complete (equivalent to conventional adaptation) gain reduction take place (Fig. 2). At the shortest backstep durations tested (16 ms for monkey SP and 32 ms for monkey CR), few experiments produced percentage gain changes that were not less than those produced by conventional adaptation (Fig. 2C). Between these shortest durations and 80 ms, there was a gradual increase in the number of experiments in which the percentage gain change was not significantly less than that produced by conventional adaptation.

A similar critical interval after the saccade was revealed with the delayed backstep paradigm. In those experiments, if the backstepped target became visible >64 ms after the saccade in monkey SP or >112 ms after the saccade in monkey CR, the amount of gain reduction was sharply reduced (Fig. 5). Therefore the target had to be visible ~80 ms after the target was stepped backward for substantial gain reduction to occur.

The period well after (up to 750 ms) the saccade

Although an error signal lasting ≥80–100 ms after the saccade is the most effective in causing adjustments in saccadic gain, the delayed backstep experiment suggests that a visual error occurring well after the saccade can still drive adaptation. For both monkeys, re-illumination of the target as much as 752 ms after the saccade caused a clear gain reduction (Fig. 5). At 752 ms, the gain reduction for monkey SP averaged 11.4% whereas the gain reduction for monkey CR averaged 8.7%.

Experiments with human subjects have produced similar results. When the target was turned off by a saccade and re-illuminated later at a backstepped location, substantial gain reductions occurred for re-illumination delays of 400 ms in most subjects and as late as 600 ms in some subjects (Fujita et al. 1996; Minakawa et al. 1997). As is apparent from the inset of Fig. 5, which plots their human data in our format, Minakawa et al. (1997) also found that the degree of adaptation varied according to how long after the saccade the backstepped target was re-illuminated. They modeled the time course of this effect as a single, exponentially declining process, which they viewed as similar to the progressive decay of working memory with time.

The results of our brief backstep experiments also suggest that errors occurring ≥300 ms after the saccade can have modest effects on saccadic gain adaptation. The data in Fig. 2C show that between 14.1% (monkey CR) and 43.2% (monkey SP) of the experiments at backstep durations of 304 ms produced percentages of change in gain that were significantly less...
than those of conventional adaptation (one-way ANOVA, $P \leq 0.05$). Therefore backward steps with durations of $\geq 300$ ms would be expected to produce small increases in the percentage of change in gain, especially in monkey SP. Unfortunately, monkey SP is no longer available to be tested.

The data from our experiments do not distinguish between two different post-saccadic error requirements. To produce the most robust adaptation, the error must be present only during the interval between $-80$ to $-100$ ms or must it be present for a total of at least $80-100$ ms? The delayed backstep experiments do, however, indicate that even if the error signal lasts for longer than $80-100$ ms but starts more than $100$ ms after the saccade, the amount of adaptation is substantially reduced. Therefore if the error does need to last at least $80-100$ ms, it apparently must be present during the first $80$ ms after the saccade to have its greatest effect.

Our observation that target conditions occurring well after a saccade has ended can affect gain adaptation is consistent with the data of Wallman and Fuchs (1998). In their study, a target was displaced backward for only $120-280$ ms then returned immediately to its non-backstepped position before any corrective saccade occurred. Under those circumstances, the amount of gain reduction was about half of that produced by conventional adaptation. The present data suggest that in the Wallman and Fuchs (1998) study the initial target backstep created an error signal that attempted to drive a gain reduction. However, the later return of the target to its initial displacement reduced the error to zero, signaling that no gain adaptation was necessary. Because we have shown that later error signals are less effective in causing gain changes than are those occurring within $80-100$ ms of the saccade (Figs. 2 and 5), the initial error signal driving a gain reduction dominated.

**Nature of the error signal driving adaptation**

From our experiments, it still is unclear whether the visual error signal after the first targeting saccade is the sole driver for saccadic adaptation or whether the post-saccadic error produces corrective saccades from which an additional error signal is derived. In representative experiments from Fig. 1D, brief backsteps (48 ms), which produced only modest gain reduction, elicited corrective saccades that were substantially different both in direction and latency from those elicited in conditions producing robust gain changes, i.e., 304-ms brief backsteps (Fig. 3). From these results, it could be argued that the unusual corrective saccades for the briefest backsteps accounted, at least in part, for the poor adaptation.

However, the corrective saccades for intermediate backsteps of 112-ms duration also differed substantially from those accompanying adaptation to 304-ms backsteps. Yet the amount of gain reduction produced by 112- and 304-ms backsteps was not statistically different. These latter data suggest that the gain reduction was not dependent on corrective saccades after all. Rather, because gain reduction was the same in these two backstep conditions, the error signal driving adaptation also must have been the same, i.e., the visual error that was present in the first 112 ms following the saccade.

Others also have pointed out that the size and direction of corrective saccades depend on how long after the saccade an error signal is available. Deubel et al. (1982) showed that if the saccade goal is shifted within 60 ms after the end of the primary saccade to the target step, the first corrective saccade will take the shift into account. Similar experiments by Becker and Fuchs (1969) put the window during which a target displacement will affect a corrective saccade at 70 ms. This 60- to 70-ms window is very similar to the 80–100 ms post-saccadic interval after which there is considerably less effect on saccadic gain adaptation (Figs. 2C and 5C). These data suggest that the error signal used for determining the size of corrective saccades has temporal characteristics similar to the error signal that drives saccadic adaptation. However, the efficacy of the error signal producing saccadic gain adaptation does not appear to be the same as that of the signal that influences the corrective saccade. For example, if the target steps backward only briefly before returning to its initial displacement, a substantial gain reduction still occurs even though there are very few, if any, backward corrective saccades (Wallman and Fuchs 1998).

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