Effect of Visual Error Size on Saccade Adaptation in Monkey

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Submitted 10 April 2002; accepted in final form 16 April 2003

Robinson, Farrel R., Christopher T. Noto, and Scott E. Bevans. Effect of visual error size on saccade adaptation in monkey. J Neurophysiol 90: 1235–1244, 2003; 10.1152/jn.00656.2002. Saccades that consistently over- or undershoot their targets gradually become smaller or larger, respectively. The signal that elicits adaptation of saccade size is a difference between eye and target positions appearing repeatedly at the ends of saccades. Here we describe how visual error size affects the size of saccade adaptation. At the end of each saccade, we imposed a constant-sized error by moving the target to a specified point relative to eye position. We tested a variety of error sizes imposed after saccades to target movements of 6, 12, and 18°. We found that the size of the gain change elicited in a particular experiment depended on both the size of the imposed postsaccade error and on the size of the preceding target movement. For example, imposed errors of 4–5° reduce saccades tracking 6, 12, and 18° target movements by an average of 18, 35, and 45%, respectively. The most effective errors were those that were 15–45% of the size of the initial target eccentricity. Negative errors, which reduce saccade size, were more effective in changing saccade gain than were positive errors, which increased saccade size. For example, for 12° target movements, negative and positive errors of 2–6° changed saccade gain an average of 35 and 8%, respectively. This description of the relationship between error size and adaptation size improves our ability to adapt saccades in the laboratory and characterizes the error sizes that will best drive neurons carrying the adaptation-related visual error signal.

INTRODUCTION

If voluntary rapid eye movements, called saccades, are repeatedly inaccurate they will change, or adapt, so that they become more accurate. This is true in both humans (Deubel et al. 1986; McLaughlin 1967; Miller et al. 1981) and monkeys (Straube et al. 1997). Saccade adaptation is necessary for clear vision because it produces saccades that accurately aim the small fovea at targets of interest. Visual feedback cannot provide this accuracy because saccades are too brief to allow vision to guide them to their targets.

To understand the mechanism of saccade adaptation, we must characterize the error signal that tells the brain that saccades are inaccurate. A good description of this error signal will be useful because it will enable us to produce strong adaptation in the laboratory and will tell us what response characteristics we can expect in the neurons that carry this signal.

Current data provide descriptions of several important features of the adaptation-related error signal in monkeys. It originates when, at the end of saccades, targets repeatedly appear eccentric to the center of gaze. As with human saccade adaptation (Fujita et al. 2002), monkey adaptation is impaired when the target does not appear beginning within ~100 ms of saccade end. Adaptation is also impaired if the target appears for <80 ms (Shafer et al. 2000). Further, the error signal arises from retinal regions near the fovea. Movement of a large visual background during adaptation has little or no effect on the size of the elicited gain change (Robinson et al. 2000). The error signal could plausibly originate with the performance of corrective saccades because they reliably follow inaccurate saccades. Current data indicate, however, that corrective saccades are not necessary for adaptation. Adaptation of substantial (Wallman and Fuchs 1998), and even normal (Noto and Robinson 2001), size occurs when we reduce or eliminate corrective saccades by manipulating target presentation. Finally, the error signal for saccade adaptation does not depend on extra-retinal signals such as extraocular muscle afference (Lewis et al. 2001; Seeberger et al. 2002).

A potentially important feature of the error signal that we still know little about is its size. How far from the center of gaze must a target repeatedly appear after saccades to elicit adaptation? The experiments described here characterize the dependence of adaptation size on the size of postsaccade errors. We found that, despite variability, the size of both the postsaccade error and the initial target eccentricity affect the size of saccade adaptation. We have previously presented a preliminary report on these findings (Robinson and Noto 2000).

METHODS

Animal preparation and training

Subjects were four adolescent male rhesus macaques (Macaca mulatta), monkeys 1–4. We prepared the monkeys for this study in a sterile surgery and under general anesthesia. Before surgery, we sedated each monkey with an intramuscular injection of ketamine HCl (10 mg/kg) and then used inhalation anesthesia (isoflurane, 1.0–2.0%) during surgery. In surgery, we implanted each monkey with a three-turn coil of fine Teflon-coated wire around one eye. The ends of the wire terminated in a socket fixed to the top of the skull with stainless steel screws and dental acrylic. In the same surgery, we attached three acrylic lugs to the monkey’s skull so we could stabilize the head during eye-movement recordings.

After the monkey recovered from surgery, we trained it to use saccades to track a moving target spot by monitoring eye position with the eye coil (Fuchs and Robinson 1966; Robinson 1963).
training, a monkey received a dollop of applesauce from a feeding tube near its mouth when it directed its eyes to within 1° of a small (0.3°) spot of light from a laser diode projected onto a screen 57 cm in front of it. A computer set the position of the spot on the screen by controlling two mirror galvanometers off of which the spot’s image reflected. Training and subsequent data collection took place ~5 days/week with monkeys in a darkened sound-attenuating booth. During every experiment, the target moved only along the horizontal meridian and never moved to >20° from the center of the screen.

Data collection and analysis

We began collecting data after a monkey was trained well enough to reliably make saccades to track ≥3,000 target steps in one 3-h stay in the booth. During data collection, an A/D board digitized voltages proportional to target and eye position at 1 kHz. A Macintosh Power PC computer measured the size of target and eye movements as they occurred. We defined the beginning and end of a saccade as the points at which eye velocity exceeded and fell below 30°/s, respectively. During adaptation, we increased the size of the reward window from the 1° we used during training to 2°. This made no difference in the monkey’s behavior because by the time we collected data from a monkey, it was very well trained.

In the experiments described here, we collected data from each monkey in a series of separate adaptation sessions. Each session consisted of data from saccades in only one horizontal direction. Each time a monkey was in the booth, we could collect data in two concurrent adaptation sessions, one adapting leftward saccades and the other adapting rightward saccades. We could elicit and analyze the adaptation of leftward and rightward saccades independently because adaptation of saccades in one direction does not influence saccades in the opposite direction (Albano 1996; Deubel et al. 1986; Frend and van Opstal 1997; Miller et al. 1981; Straube et al. 1997; Weisfeld 1972). Consistent with these previous studies, concurrent adaptation sessions in our work here could, and often did, produce adaptations of different sizes.

Each adaptation session followed the same procedure. We first recorded ~30 saccades in each direction that tracked normal targets, i.e., those that did not move at the end of each saccade. These were preadaptation saccades. Next we recorded between ~400 and ~2,800 saccades in each direction as they followed targets that moved at the end of every saccade. These were adaptation saccades. We describe these adapting target movements in detail in the following text. The number of adapting target movements that we presented varied depending on how quickly the size of the monkey’s saccades changed and how many saccades the monkey was likely to make during a particular session. After presenting all of the adapting target movements in a session we again recorded ~30 saccades to normal target movements. These were postadaptation saccades.

Throughout each experiment, the computer recorded the size and direction of every target movement and subsequent saccade in the order they occurred. It also recorded saccade gain calculated by dividing saccade size by target movement size. We exported recorded target and saccade data to commercial programs Excel (Microsoft) and IGOR Pro (Wavemetrics) for analysis. As a backup, we also used a PCM adapter (Vetter 4000A) to record voltages proportional to target and eye position on video tape.

Eliciting saccade adaptation

Our technique for eliciting saccade adaptation was a modification of the intra-saccade target movement procedure first used by McLaughlin (1967). In this procedure, saccade onset triggers target movement during the saccade. This intra-saccade movement results in a difference between eye and target positions, i.e., an error, at the end of the saccade. Errors that make saccades smaller are called negative errors. Those that make saccades larger are positive errors. Repeated negative or positive errors changes saccade size in humans (Deubel et al. 1986; McLaughlin 1967; Miller et al. 1981) and monkeys (Straube et al. 1997). In monkeys, these changes persist for 20 h in the dark after adaptation and so are not a strategy employed by the monkey to stay on target and continue receiving a reward (Straube et al. 1997).

In the usual adaptation procedure, the size of the intra-saccade target movement is fixed. As saccade size adapts, the mean size of the post-saccade error decreases. In the experiments described here, we modified this technique so that post-saccade error size remained constant regardless of saccade size. To do this, a computer measured eye position at the end of each saccade and moved the target to a point that was a specified distance from that eye position.

Our procedure presents the error at the end of the saccade while the usual adaptation procedure presents the error before the saccade ends. It is extremely unlikely that the later appearance of the error in our procedure changed the amount of adaptation elicited. In our studies, the target is moving to its final position for only a few milliseconds after the end of the saccade, e.g., 3.5 ms in Fig. 1D. Previous work does not examine exactly this situation but does show that a post-saccade error must persist for >32 ms to affect adaptation (Shafer et al. 2000). We infer from this that the target in our studies would have to be outside of its final position for much longer than a few milliseconds to affect adaptation.

Figure 1 shows examples of saccades to 12° rightward target movements and the subsequent post-saccade target movements that imposed a 1° negative error. Figure 1A-C, shows records of saccades at the beginning, middle, and end of adaptation, respectively. When the velocity of each saccade falls to 30°/s, the target moves to a point 1° to the left of where the eye was when its velocity was 30°/s. Note that visual error remains the same size as saccades become smaller. Figure 1D illustrates in detail the target movement at the end of the saccade.

As Fig. 1D shows, the target movement begins before the eye stops moving. Thus the post-saccade visual error presented to the monkey is slightly larger than the post-saccade target movement that we specified. For example, we specified a 1° intra-saccade movement in the experiment illustrated in Fig. 1, but the actual visual error is 1.2°. We measured the actual size of the visual error presented in each adaptation session by measuring the errors following ~50 saccades in that session. To do this, we digitized the records of these movements from the video tape record and analyzed them with a custom interactive program that allowed us to measure the difference between target and eye positions when eye velocity fell to 5°/s, the smallest eye velocity detectable with the program’s velocity resolution. In the measurements presented in the following text, the error size for each adaptation session is the average of the measurements of post-saccade errors measured from these digitized records. As clear in Fig. 3, the SDs for these averages were typically quite small.

We imposed negative errors after initial target movements of 6, 12, or 18° and positive errors after initial target movements of 12°. Negative errors after 6° target movements ranged from 0.25 to ~5°, those after 12° target movements ranged from 0.25 to ~15°, and those after 18° initial target movements ranged from 0.25 to 16°. Errors after 12° target movements that were larger than 12° placed the target on the side of the eye that was opposite to its initial position. For example, for adapting rightward saccades, the target would move quickly 12° to the right. After the monkey made a 12° rightward saccade to look at it, the target would move 14° left, ending 2° to the left of its original position. Positive errors after 12° target movements ranged from 0.25 to ~8°.

Each time a monkey was in the booth, we presented the same size of initial target movement and post-saccade target movement for adaptation of both left- and rightward saccades. We sorted the data from all adaptation sessions into four categories, those that presented negative errors after 6, 12, or 18° initial target movements and those that presented positive errors after 12° target movements. We subdivide each of these categories into three error size groups, small,
intermediate, and large. We placed the borders between these categories to separate error sizes into ranges that elicited the same kind of gain changes. Small errors elicited both large and small gain changes. Intermediate errors elicited large gain changes. Large errors elicited both large and small gain changes. The vertical dashed lines in Fig. 3 mark the borders of these groups. We compared the means of these groups with a $t$-test assuming unequal variance and used the Bonferroni/Dunn correction for repeated tests.

The eye-coil technique provided stable and precise measurements of eye position, but our calibration procedure limited the accuracy of our measurements. We calibrated the voltages representing eye position on a display showing eye and target positions in two dimensions. We adjusted the gain, offset, and direction of the eye-position signals so that when the monkey looked at the target, the spot representing eye position overlapped completely with the spot representing target position. We could reliably detect offsets of $\pm 0.25°$ between the two spots but may not have always detected smaller offsets. Ambiguity of $\pm 0.25°$ in error size could not significantly affect our results for most error sizes. Any error in the range $\pm 0.25°$ from 0, however, could be either positive or negative thus making it impossible to be sure that we properly interpreted errors of this size. We have therefore eliminated from analysis the 12 adaptation sessions that presented errors in the range of $\pm 0.25°$.

Measuring adaptation

We assessed saccade size as gain, i.e., saccade size divided by target movement size. We used a least-squares technique to fit an exponential curve to the relationship between saccade gain and the order number of each saccade in an adaptation session. The asymptotic value of this fit curve represents a good estimate of the mean gain that saccades would reach when adaptation was complete (Straube et al. 1997). We calculated the percent gain change elicited in each adaptation session using this asymptotic value. Figure 2 shows a graph of saccade gain versus saccade number from a typical adaptation session in which we adapted the gain of a monkey’s rightward saccades. Saccade number refers to the number of saccades the monkey made in this session, i.e., the number of rightward saccades. We used the asymptotic value of an exponential curve fit to these data to calculate percent gain change elicited in this session. Calculating percent gain change with this asymptotic value provided the same measure for every adaptation session regardless of how many saccades the monkey made. We preferred this to measuring percent gain change with postadaptation saccade size. Analysis after data collection shows that each adaptation had progressed toward its asymptotic value by a different amount. Thus measuring percent gain change with postadaptation saccade size assesses adaptation in each session after a different amount of progress.

As we describe in DISCUSSION, we also calculated percent gain change using the gain of the preadaptation and postadaptation saccades. We used this second method to check that the results we obtained using the asymptotic value did not distort our results.

All surgical and behavioral training procedures were approved by the Animal Care and Use Committee at the University of Washington. The veterinary staff of the National Primate Research Center cared for our animals. Our monkeys were housed under conditions that comply with National Institutes of Health standards as stated in the Guide for...
the Care and Use of Laboratory Animals (DHEW Publication NIH85-23 1985) and with recommendations from the Institute of Laboratory Animal Resources and the American Association for Accreditation of Laboratory Animal Care.

RESULTS

We measured the visual error size and percent gain change in 182 adaptation sessions in three monkeys, 56 in monkey 1, 66 in monkey 2, and 60 in monkey 3. (Monkey 4 participated in another experiment described in the following text.) The gain of each monkey’s saccades before each adaptation session was within the normal range with mean preadaptation gains for all sessions of 0.94, 0.98, and 0.95 for monkeys 1–3, respectively. Within each adaptation session there was little variation in the size of the imposed postadaptation error. The mean SD of error size for all sessions in monkeys 1–3 were, 0.15, 0.27, and 0.29°, respectively.

The size of the gain change elicited in a particular adaptation session varied with the size of visual error and the size of initial target movement. In the following text, we first describe the adaptation elicited by negative errors and then the adaptation caused by positive errors.

Effect of negative error size on gain change

Figure 3 summarizes the relationship between error size and percent gain change for the three sizes of initial target movement that we examined. Each point in Fig. 3 represents the result from one adaptation session.

6° INITIAL TARGET MOVEMENTS. Figure 3A shows that of the 11 sessions with error sizes <2°, 10 reduced saccade gains by 19–42%. The mean gain reduction for all 11 sessions was 27%.

The 12 sessions with error sizes 2–4° caused gain reductions in the range from 23 to 51%. The mean reduction of these sessions was 30% and was not significantly different from the mean reduction caused by errors <2° (P > 0.4).

The 12 sessions with errors >4° elicited gain reductions in the range from 4 to 35%. The mean of these reductions was 19%, which was significantly smaller than the reductions elicited by 2–4° errors (P < 0.02) but indistinguishable from the reductions elicited by errors <2° (P < 0.2).

12° INITIAL TARGET MOVEMENTS. Figure 3B, left, shows that of the 27 sessions with errors <2°, 25 caused gain reductions in the range from 17 to 57%. The mean reduction caused in all 27 sessions was 32%.

Of the 24 sessions with errors 2–6°, 23 elicited gain increases of 25–62% with an average reduction of 35%, which was not significantly different from the reductions elicited by errors <2° (P = 0.36).

The 13 sessions with errors >6° elicited gain decreases of 0–38% with an average reduction of 30%, which was significantly smaller than the reductions caused either by errors <2° (P < 0.01) or by those >2° (P < 0.005).

18° INITIAL TARGET MOVEMENTS. Figure 3C shows that the 10 sessions with errors <2° elicited gain reductions of 12–43% with a mean reduction of 32%.

The 35 sessions with 2–12° errors elicited gain reductions of 19–60% with a mean reduction of 42%, which was significantly larger than the reduction caused by errors <2° (P < 0.05).

The four sessions with errors >12° elicited gain changes from an increase of 4% to a reduction of 15% with a mean reduction of 7%, which was significantly smaller than the reductions caused by either 2–12° (P < 0.002) or those <2° (P < 0.005).

Effect of positive error size on gain change

Figure 3B, right shows that in 8 of the 13 adaptation sessions with positive errors <2°, saccade gain reduced, i.e., changed in the wrong direction. Among the remaining 5 sessions, the largest gain increase was 21%. The mean gain change of all 13 sessions was a 1.8% decrease.
There were 17 sessions with positive errors in the range 2–6°, of which 3 elicited gain reductions and 14 elicited gain increases. The range of these gain changes was from a decrease of 11% to an increase of 29%. The mean gain change of all of these sessions was an 8% increase, which was significantly larger than the changes elicited by <2° errors ($P < 0.04$).

**FIG. 3.** The relationship between error size and percent gain change. Each point represents the result from 1 adaptation session. Different symbols represent results from different monkeys. The SD for the average error size is marked as a horizontal line on each point. For most points, the SDs are so small that they are not visible beyond the symbol. The vertical dashed lines mark the ranges of error sizes we discuss in the text. A: initial target movements of 6°; B: initial target movements of 12°; C: initial target movements of 18°.
Of the eight sessions with positive errors in the range from 6 to 8.2°, the largest positive error we measured, all elicited gain increases, which ranged from 9 to 21%. The mean gain increase produced by errors in this range was 14%, which was not distinguishable from the mean change elicited by 2–6° errors (P > 0.05) but was significantly larger than the change caused by errors <2° (P < 0.001).

Positive errors <2° were often not effective in increasing saccadic size and were significantly less effective than negative errors <2° in changing saccade size (P = 0.005, comparing the absolute value of percent gain change caused by negative errors <2° to the percent change caused by positive errors <2°). Positive errors of 2–6° were more effective than positive errors <2° but were significantly less effective than negative errors of 2–6° in changing gains (P < 0.001, comparing the absolute value of percent gain change caused by 2–6° positive errors to the percent change caused by 2–6° negative errors). Positive errors 6–8.2° were as effective at increasing gain as were 2–6° positive errors. They were, however, significantly less effective than negative errors 6–8.2° (P < 0.003, comparing the absolute value of the percent gain change caused by 6–8.2° positive errors to the percent change caused by 6–8.2° negative errors). The largest positive errors we tested were the most consistently effective in increasing saccade size. Thus we have not tested positive errors large enough to tell us how large positive errors must be to be ineffective.

**Initial target movement size influences adaptation**

The relationship between error size and gain change depends, in part, on the size of the initial target movement. Figure 4A illustrates this by overlapping gain changes from three different initial target movement sizes. Despite variability, there are two differences evident between gain changes in sessions with different initial target movement sizes. First, gain reductions in sessions with 6° initial target movement are generally smaller than the gain reductions in sessions with 12 and 18° target initial movements. This is evident in Fig. 4A because despite much overlap, the green triangles that represent sessions with 6° initial target movements are generally nearer to 0 than the red and blue points that represent 12 and 18° initial target movements, respectively.

Second, as negative error size increases in Fig. 4A, the size at which gain reductions start to become smaller is different for 6, 12, and 18° initial target movements. For example, for ~5° errors there are five sessions with 6° initial target movements that elicited gain reductions <20% but only one session with 12 and 18° initial target movements. For ~8° errors, the red points representing 12° initial target movements are generally nearer to 0 than the blue points representing 18° initial target movement.

Both the smaller gain reductions elicited after 6° target movements and the different responses to large errors for the three different target movement sizes are apparent in Fig. 4A, inset. This inset graphs a nine-point smoothed curve of the gain change data in Fig. 4A.

To confirm that adaptations of saccades to 6, 12, and 18° initial target movements are different we fit each of these three data sets with this log normal model

\[ Y = Ae^{(-t/\tau)\ln(2)} \]

We used an F test to compare the curves fit to each data set to the curves fit to the other two sets. These comparisons show that the data sets representing adaptation of saccades to 6, 12, and 18° target movements are each significantly different from one another (each P < 0.02).

Figure 4B shows the same data as in A but expresses error size as a percentage of initial target movement. For example, we plot a 6° error following a 12° initial target at 50 on the abscissa on this graph. As apparent in Fig. 4B, the data sets representing adaptation of saccades to 6, 12, and 18° initial target movements overlap extensively when plotted like this. We compared the 6, 12, and 18° data sets in Fig. 4B with the test described in the preceding text for the data in A. We found that the set representing adaptation of saccades to 12° target movements was not distinguishable from either the 6° or the 18° set (each > P = 0.2). The 6° set was distinguishable from the 18° set (P < 0.02). We interpret this difference to be a consequence of the fact that adaptation of saccades to 6° targets usually produce smaller gain changes than do adaptations to 18° targets.

The fact that the 6, 12, and 18° data sets overlap more in Fig. 4B than they do in A supports the idea that the gain change elicited by a particular error size is determined by the size of the error relative to the size of the initial target movement. Figure 4B, inset, shows the overlap of the 9-point smoothed curves of the gain change data in B.

From this point of view, error sizes <10% of the initial target size elicit quite variable gain changes ranging from ~1 to 50% with a mean of ~30%. Error sizes 15–45% elicit more consistent gain changes of ~20–60% with a mean of ~40%. Error sizes >45% elicit gain changes whose sizes decrease with increasing error size.

**Constant error size elicited maximum gain reduction**

Normally saccades that repeatedly overshoot their target will become smaller until they end on their targets. When this happens, there is no longer an error signal to drive adaptation so adaptation stops. In contrast to the normal situation, this study imposed error signals whose size did not change regardless of how well adapted saccades became. Despite this, saccade gain stopped adapting (e.g., Fig. 2). Why did adaptation stop when error size remains constant? The simplest answer is that the adaptation mechanism had changed saccade size as much as it could. If this were true, then the largest gain changes elicited in these experiments show the maximum gain change that the adaptation mechanism can make.

Before we can accept this conclusion we must eliminate an alternative interpretation. Perhaps as adapting saccades become smaller, the size of the imposed constant error represents too large an error, relative to target movement to effectively drive adaptation. If this were true, we would be able to first use a large error to reduce the size of a monkey’s saccades to an asymptotic value and then cause a further reduction in saccade size by presenting a smaller error.

We tested this prediction in 10 additional adaptation sessions, 2 in monkey 1, 4 in monkey 3, and 4 in monkey 4. We used constant amplitude negative errors 1.8–4.2° (15–35% of initial target movement size) to adapt saccades to 12° target movements...
movements. After saccade gain seemed to have stopped adapting as judged from watching the decrease in saccade gains measured by the computer, we reduced the size of the imposed error to 0.6–2.0° depending on the session. The second, smaller, errors were 33–57% of the size of the initial, larger, errors. Depending on the session, the monkeys made 69–214 (mean = 123) saccades to targets followed by the smaller error.

Figure 5 shows saccade gains in a session with monkey 3 in which the first, large error was 2.8° and the smaller error presented later was 1°. The monkey made 175 saccades followed by the smaller error. In this and the other nine session in this experiment, the imposition of the smaller error elicited no decrease in saccade gain beyond that already achieved by the larger error. The gains of the first and last 30 saccades that the monkey made while adapting to the smaller error were not

**FIG. 4.** Superimposed data from adaptation sessions with 6, 12, and 18° initial target movement sizes showing the relationship between error size and percent gain change. Percent gain change was calculated from the asymptotes of exponential curves fit to saccade gains. Each point represents the gain change from 1 adaptation session. - - - - , a gain reduction of 7%, that may occur as a consequence of the monkeys making many saccades in the dark (see DISCUSSION). A: error size expressed in degrees. B: error size expressed as a percent of the size of the initial target movement. Insets: the relationship between error size and gain change with 9-point smoothed curves of the data in the large graphs.
significant difference in any of these experiments (average gains of 1st 30 and last 30 saccades across 10 experiments = 0.65 and 0.65, respectively; $P = 0.06 - 0.97$; mean $P = 0.42$).

In contrast, the same method for assessing gain change showed significant changes at the start of the monkey’s adaptation to the larger error. We examined the same number of saccades from the beginning of adaptation to the large error that the monkey made during adaptation to the smaller error, e.g., 175 in the session in Fig. 5. The average gain of the last 30 saccades in this sample were significantly smaller than the average gain of the first 30 in all 10 experiments (mean gains of the first and last 30 saccades across 10 experiments = 0.92 and 0.82, respectively, every $P < 0.001$). Thus the number of saccades that the monkey made followed by the smaller error was sufficiently large to elicit adaptation.

**DISCUSSION**

The results describe here characterize the relationship between the size of the visual error following saccades and the size of the gain change elicited by that error. We assessed this relationship by imposing an error whose size was constant throughout adaptation. This technique contrasts with normal saccade adaptation in which error size decreases as saccades adapt. Despite this difference, we think that constant error adaptation engages the same adaptation mechanism as does normal adaptation. Gain changes during constant error adaptation follow the normal exponential course. Variability in saccade size is similar during normal and constant error adaptation. Finally, as described in the following text, the one quantitative difference between normal and constant error adaptation is small and easy to account for.

The adaptation elicited by constant-sized negative errors may be larger than that elicited by normal adaptation. For example, previous work reports that normal adaptation with 30% negative errors reduces gain by an average of $\sim 25\%$ as measured by the asymptote of a fit exponential (Straube et al. 1997, their Table 1). In the present study, constant negative errors of 25–35% elicit an average gain reduction of 35% in the gain of saccades to 12° targets. The most straightforward explanation for this difference is that during adaptation to constant errors, a significant error follows every saccade. During normal adaptation error size decreases so that given the variability of saccade gain during adaptation, some saccades are not followed by errors large enough to drive adaptation.

Constant positive error may be less effective than normal positive errors in eliciting gain changes. Normal 30% positive errors elicit an average gain increases of 18% (Straube et al. 1997, their Table 1), but in the present study, positive errors of 25–35% following saccades to 12° targets elicited an average gain increase of only 8%. We currently have no explanation for the difference between the effectiveness of negative and positive constant errors relative to normal errors.

There is one indication that adaptations to constant errors have larger rate constants than adaptation caused by normal errors, but our experience indicates that this may not be true. The rate constants of adaptations elicited by constant errors in this study vary widely, $<100$ to $>1800$ saccades. There was no clear relationship between rate constant and error size. Straube et al. (1997) report that normal 30% negative and positive errors elicit adaptations with average rate constants of 354 and 324 saccades, respectively (their Table 1). In contrast, the adaptations to constant negative and positive errors of 25–35% in the present study elicit adaptation with average rate constants of 894 and 1,210 saccades, respectively. In the numerous monkey saccade adaptations measured in our laboratory after publication of the Straube et al. (1997), we have seen that the rate constant of normal adaptations can vary from 100 to 2,000 saccades from day to day and monkey to monkey. In view of this variability, we are not willing to conclude from our current data that constant error adaptation has longer rate constants than normal adaptation.

As Fig. 3 shows there is no systematic difference between

**FIG. 5.** A record of saccade gain during 1 of 10 adaptation sessions in which we imposed a smaller error after adaptation to a larger error. In this session, the monkey tracked 175 target movements followed by 1° errors after adapting to a 2.8° error. The 1° error elicited no further adaptation. The horizontal brackets under the data show which groups of 30 saccades we measured to assess gain change during adaptation to 2.8 and 1° errors.
the three monkeys in their response to different error sizes. The gain change elicited by a particular error size is variable even in a single monkey tracking one initial target movement size. This variability is similar to that we observe in normal adaptations. In particular it is not the result of our presenting different combinations of conditions during simultaneous left- and rightward adaptation sessions because we always presented identical conditions in simultaneous adaptation sessions. Despite the observed variability, there is a clear relationship between error size and percent gain change (Figs. 3 and 4).

This relationship is similar for the three initial target movement sizes we tested with negative errors. Errors $<2^\circ$ produce a wide range of gain reductions with most, but not all, sessions producing substantial reductions. Errors $>2^\circ$ consistently produce large gain reductions. The largest error size that consistently produces large gain reductions is different for different initial target movement sizes.

There are two possible reasons that errors $<2^\circ$ produce such variable gain reductions. The adaptation mechanism may simply be variable in its response to small errors. It may also be that the adaptation mechanism responds consistently to small errors and that the variability in our data are a consequence of the $\pm 0.25^\circ$ uncertainty in our calibration procedure. Our current data cannot distinguish between these two alternatives.

The measure we used to assess gain change, the asymptote of an exponential curve fit to gain change, is not a common measure of adaptation. To determine if this technique distorted our findings, we also calculated percent gain change in each adaptation session using the gain of postadaptation saccades (see Fig. 2). The regression of the two measurements of gain change has a slope of 0.62 and an $R^2$ value of 0.79. Thus gain changes measured with postadaptation saccades are $\sim62\%$ of those measured with the asymptote, and the two measures are well correlated with one another. It makes sense that gain changes measured with postadaptation saccades are smaller than those measured with the asymptote in Figs. 3 and 4. Postadaptation measurements assess adaptation size before gain has fallen all of the way to its asymptotic value.

The major features of the relationship between error size and adaptation size allow three inferences about the mechanism that adapts saccade size. First, the size of the adaptive gain change is influenced by both error size and the size of the initial target movement. Second, the adaptation mechanism is limited in its ability to change saccade size and we now know, at least approximately, what that limit is. Third, the adaptation mechanism is more sensitive, and responds more strongly, to negative errors than to positive errors. We discuss each of these inferences in the following text. First, however, we explain why it may be necessary to compensate our data because reductions in saccade gain occur whenever monkeys make many saccades in the dark as they did during these experiments.

Compensating for the effect of the monkeys making many saccades in the dark

In Fig. 3B just below the center of the graph are a group of points representing 10 adaptation sessions in which the monkeys saw small positive errors after each saccade but which produced a small decrease in saccade size. These decreases in saccade size are maladaptive because positive errors indicate that the saccades are too small, yet saccade size becomes smaller still during adaptation. Earlier work shows that larger positive errors do, in fact, increase the size of monkey saccades (Straube et al. 1997). Why did small positive errors in our experiments often produce reductions in saccade size?

We propose that small positive errors elicit no adaptation. The small gain reductions in the sessions with small positive errors occurred because the monkeys made many saccades in the dark. Previous work shows that saccade gain falls by $4\%$–$7\%$ when monkeys made many (2,000–7,000) saccades in the dark to normal target movements, i.e., those not followed by a posttracking saccade error (Straube et al. 1998).

In our experiments, monkeys probably made fewer saccades than did the monkeys in the Straube et al. experiments. In the 10 adaptation sessions in which we imposed positive errors $<2^\circ$, the monkeys made saccades to an average of 662 target movements in one direction. Monkeys made roughly twice this number of saccades to track initial target movements during each experiment because each experiment consisted of two simultaneous sessions that each measured only left- or rightward saccades. Monkeys also made corrective saccades following every saccade in either direction during adaptation. Thus the monkeys in these experiments made $\sim2,500$ saccades in each experiment.

If, as we propose, gain fell in sessions with small positive errors only because monkeys made many saccades in the dark, then the true baseline from which we should measure gain changes is a gain reduction of $\leq7\%$. We have represented the largest potential offset of the baseline with the dashed line at 7% in Fig. 4. Displacing the baseline in this way increases the size of the changes elicited by positive errors by $\leq7\%$ and decreases the size of the errors elicited by negative errors by $\leq7\%$. Even if this entire shift is appropriate, it is not large enough to change any of the major findings of these experiments.

Both error size and initial target movement size affect gain change

As Fig. 4A shows, the repeated appearance of targets at a particular location on the retina elicits gain changes of different sizes when this error follows saccades to targets at different distances. For example, $5^\circ$ negative errors elicit mean gain changes of $\sim15$, $\sim35$, and $45\%$ after saccades to targets that are 6, 12, and $18^\circ$ eccentric of initial eye position, respectively. Adaptive gain reductions of saccades to 6, 12, and $18^\circ$ targets are statistically distinguishable. We conclude from these observations that initial target distance influences the amount of gain change during an adaptation.

Figure 4B shows that the 6, 12, and $18^\circ$ data sets overlap extensively when we express error size as a percentage of initial target distance. Transformed in this way only the 6 and $18^\circ$ data sets are statistically distinguishable from one another. Thus we can reasonably summarize the relationship between error size, target distance, and the size of elicited adaptation by expressing error size as a percent of initial target distance if we recognize that saccades to $6^\circ$ targets adapt less than saccades to 12 and $18^\circ$ targets.
Limit of saccade size adaptation

The most straightforward interpretation of the fact that adaptation stopped in the presence of a constant error is that it had reached the limit possible in response to a particular error size. If this is true, why is that limit so variable? Even the error size that caused the maximum gain reductions, \( \sim 20\% \) of target eccentricity, elicited adaptations of 30–60\%. Current data do not provide an explanation for the variability in the adaptation limit, but such variability is consistent with the monkey-to-monkey and session-to-session variability of adaptation rate and size reported in earlier monkey studies (e.g., Straube et al. 1997).

Adaptation mechanism is more responsive to negative errors than to positive errors

As apparent in Figs. 3B and 4, the adaptation mechanism is more sensitive to small negative errors than to small positive errors. Even for errors large enough to elicit clear gain changes, negative errors elicit larger changes than do positive errors. Negative errors are more effective in changing saccade gain than are positive errors even if we regard gain reductions as negative errors elicit larger changes than do positive errors. Even for errors large enough to elicit clear gain changes, more sensitive to small negative errors than to small positive errors. The fact that the adaptation system responds better to negative than to positive errors may account for the fact that normal saccades are consistently hypometric (Becker 1989). Superficially the average hypometria of normal saccades is hard to reconcile with the presence of an adaptation system that, nominally, corrects for consistent inaccuracies. The gain of normal saccades is variable, however. Some normal saccades overshoot while others fall short. Our data indicate that the adaptation mechanism responds more effectively to reduce the size of the overshooting saccades than to increase the size of those that fall short. We propose that this imbalance produces normal saccades with an average gain less than one.

We gratefully acknowledge B. Brown and the veterinary care staff at the Regional Primate Research Center for excellent care of the animals. We also thank A. Fuchs, C. Kaneko, L. Ling, J. Phillips, S. Brettler, and L. Mezey for helpful comments on an earlier draft of this article. Finally, we are very grateful to R. Soetedjo for help with some of our statistical tests.

DISCLOSURES

This study was supported by National Institutes of Health Grants RR-00166 and EY-10578.

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