Characteristics of Saccadic Gain Adaptation in Rhesus Macaques

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Straube, Andreas, Albert F. Fuchs, Susan Usher, and Farrel R. Robinson. Characteristics of saccadic gain adaptation in rhesus macaques. J. Neurophysiol. 77: 874–895, 1997. We adapted the saccadic gain (saccadic amplitude/target step amplitude) by requiring monkeys to track a small spot that stepped to one side by 5, 10, or 15° and then, during the initial targeting saccade, jumped either forward or backward by a fixed percentage of the initial step. Saccadic gain increased or decreased, respectively, as a function of the number of adapting saccades made in that direction. The relation between gain and the number of adapting saccades was fit with an exponential function, yielding an asymptotic gain and a rate constant (the number of saccades to achieve 63% of the total change in gain). Backward intrasaccadic target jumps of 15, 30, and 50% of the initial target step reduced the asymptotic gain by an average of 12.2, 23.1, and 36.4%, respectively, with average rate constants of 163, 368, and 827 saccades, respectively. During 50% backward jumps, some saccades, especially those to larger target steps, became slower and lasted longer. Forward intrasaccadic jumps of 30% increased the asymptotic gain by 23.3% (average rate constant of 1,178 saccades). After we had caused adaptation, we induced recovery of gain toward normal by requiring the animal to track target steps without intrasaccadic jumps. Recovery following forward adaptation required about one third fewer saccades than the preceding gain increase. Recovery following backward adaptation required about the same average number of saccades as the preceding gain decrease. The first saccades of recovery were slightly less adapted than the last saccades of adaptation, suggesting that a small part of adaptation might have been strategic. After 50% backward jumps had reduced saccadic gain, the hypometric primary saccades during recovery were followed by hypometric corrective saccades, suggesting that they too had been adapted. When saccades of only one size underwent gain reduction, saccades to target steps of other amplitudes showed much less adaptation. Also, saccades in the direction opposite to that adapted were not adapted. Gain reductions endured if an adapted animal was placed in complete darkness for 20 h. These data indicate that saccadic gain adaptation is relatively specific to the adapted step and does not produce parametric changes of all saccades. Furthermore, adaptation is not a strategy, but involves enduring neuronal reorganization in the brain. We suggest that this paradigm engages mechanisms that determine saccadic gain in real life and therefore offers a reversible means to study their neuronal substrate.

INTRODUCTION

Some somatic movements are so slow that visual feedback and feedback from motion of the body part itself can be used to guide it to the target. If neural damage reduces the efficacy of a somatic movement, feedback can still ensure that the movement is accurate. For saccadic eye movements, however, shifts in the direction of gaze occur in as little as 30 ms and a visual feedback signal would arrive too late to influence such a rapid movement. Nonetheless, saccades are very accurate. Therefore their gain, i.e., the ratio of their amplitude to the size of a target step, must be specified precisely before the saccade begins. Furthermore, the saccadic gain must be maintained despite developmental changes and normal wear and tear on the CNS.

To study how the brain adjusts the saccadic gain, it is necessary to develop a behavioral paradigm that provokes, reversibly, changes in saccadic gain. Most investigators have used the paradigm pioneered by McLaughlin (1967): a targeting saccade is elicited and, as the saccade is en route, the target is jumped either closer or further away. When the target jumps forward during a saccade, the saccade falls short of the final target position and therefore the saccade appears to have been too small. When the target jumps backward during a saccade, the saccade seems to have been too large. Repeatedly jumping targets forward gradually increases the saccadic gain, whereas jumping them backward has the converse effect, so that, on average, saccades land progressively nearer the final target location (Deubel et al. 1986; Frens and van Opstal 1994; Miller et al. 1981; Semmlow et al. 1989; Straube and Deubel 1995). Monkeys, too, undergo saccadic adaptation in this paradigm, but more trials are required to acquire the new gain (Deubel 1987).

To use the adaptation paradigm as a tool, it is necessary first to determine its characteristics under different target step conditions. Therefore in the first part of this paper we evaluate the time course of both increases and decreases in saccadic gain. In so doing, we also provide new information about other features of adaptation toward higher and lower gain and determine whether this adaptation resembles the recovery to normal saccadic gains that occurs when previously adapted subjects track target steps with no intrasaccadic target jump.

Unfortunately, this adaptation paradigm not only changes saccadic gain, but also causes some adapted saccades to be slower than normal (Albano and King 1989). It is possible that after several hundred saccades, the slowing is simply due to the effect of fatigue on saccadic metrics (Schmidt et al. 1979). On the other hand, it could be an integral part of the adaptation mechanism used to adjust saccadic gain. Therefore in the second part of this paper we quantify saccadic slowing and examine how much of it can be attributed to fatigue. A preliminary account of this study has been reported in abstract form (Straube et al. 1994).

METHODS

Four adolescent male rhesus macaques (Macaca mulatta) were trained to follow a small target spot with the eyes. Eye movements
were measured by an electromagnetic search coil technique that had a sensitivity of 15 min of arc and a bandwidth from DC to 500 Hz (Fuchs and Robinson 1966). During aseptic surgery with the animal under inhalation anesthesia, a coil was surgically implanted on the sclera and under the conjunctiva of the left eye. During the same surgery, three lugs made of dental cement were constructed over screws in the skull so that the head could be immobilized. One monkey’s head was immobilized by means of a post implanted on the skull in line with the atlantooccipital axis. Details of these procedures can be found elsewhere (Fuchs et al. 1994; Phillips et al. 1995).

Each monkey was trained to follow a small jumping target spot with the eyes; if the eyes were within an adjustable window (\( \sim 2 \times 2^\circ \)), which moved with the target, the monkey was rewarded with a small dollop of apple sauce. Three of the monkeys were trained only with heads held (monkeys R, A, and B), whereas the fourth (monkey S) initially had been trained to make gaze shifts with head free to rotate about a vertical axis. In this study, all data were gathered with the monkey’s head held. The target was a small red laser spot, which subtended either 0.25 or 0.4\(^\circ\) on a screen that faced the monkey at a distance of 57 cm. The laser beam was deflected by two orthogonal mirrors mounted on galvanometers that were controlled by a Macintosh IIfx computer.

To produce adaptation of saccadic size, a threshold discriminator detected the onset of a saccade to an initial target step when eye velocity exceeded \( \sim 50^\circ/\text{s} \), and generated a brief pulse. This pulse served as a signal to jump the target either forward or backward. The trigger for the pulse was adjusted so that the second (adapting) target jump occurred before the peak velocity of the ongoing saccade. The computer controlled the direction and amount of the jump, which occurred for all targeting saccades in only one direction: in the opposite direction, the targets did not jump during saccades. The initial target step was varied pseudorandomly among three sizes (5, 10, and 15\(^\circ\)) within a maximum target excursion of \( \pm 20^\circ \) from straight ahead. Because target motion was limited to \( \pm 20^\circ \), larger target steps occurred somewhat less frequently than smaller ones. In each experiment, the backward or forward adapting jump was always a fixed percentage of the initial target step. However, because target steps were of different sizes, the target start and stop locations were unpredictable. For horizontal target movements, the intrasaccadic target jump was either 15, 30, or 50\% of the prior step when in the backward direction or 30\% when in the forward direction. For vertical target movements, the intrasaccadic jumps were always 30\% of the prior initial step and in the backward direction. All 45 adaptation experiments were performed either essentially in the dark (\( n = 40 \)) or in the presence of a background light with a luminance of \(<0.05 \text{ cd/m}^2\).

At the start of each experiment, we recorded 200–400 saccades to target steps of several amplitudes with no intrasaccadic target jump. These control saccades, which were in both directions, occasionally included the amplitudes expected in response to 5, 10, and 15\(^\circ\) target steps after the animal was adapted, e.g., 3.5, 7, and 10.5\(^\circ\) for 30\% backward adaptation. After the control saccades were recorded, the monkeys were subjected to the adaptation paradigm in one direction. Within 600–2,000 saccades they achieved nearly asymptotic saccadic gain, as judged by viewing saccadic amplitudes on a memory oscilloscope, and were then required to track a simple target step. This task caused recovery toward a gain near preadaptation values; recovery required another 600–2,000 saccades. Thus most experiments required the performance of 4,000–6,000 targeting saccades, including those in the direction opposite to that adapted. This regimen required the animals to work for 2.5–3.5 h. To test whether the saccadic metrics after adaptation or recovery could be attributed to fatigue, we required the same monkeys to perform a total of 5,000–6,000 saccades in response to simple target steps in both directions.

Saccadic characteristics were analyzed by interactive computer programs. Horizontal and vertical eye position and horizontal and vertical target position were digitized on-line at 1 kHz and stored. After the experiment, we displayed the digitized eye and target signals on the monitor of a Macintosh computer. The analysis program produced eye velocity signals and scrolled through the data, identifying saccades by a settable velocity criterion. The program marked the onset and offset of each saccade’s horizontal and vertical component and also pointed out the times of component peak velocities. The operator could then accept or alter the markings proposed by the computer. Only targeting saccades were accepted. If the saccade was accepted, the computer stored the metrics and timing of the saccadic components, i.e., amplitude, duration, and peak velocity, as well as the component target amplitudes, for later analysis.

After a data file of saccadic characteristics had been created, it was exported to commercial programs (Microsoft Excel and WaveMetrics Igor) for further analysis, including calculation of saccadic gain. These programs allowed us to sort saccades according to size, direction, and time of occurrence during the trial and to fit the data iteratively with exponential or linear regressions.

To document the time course of adaptation, we plotted saccadic gain against the number of the saccade in the session and fit this relation with an exponential curve (Igor 1.28, WaveMetrics). To characterize the proportion of total variance in saccadic gains accounted for by this exponential curve, we used the \( \chi^2 \) value provided by the fitting program to calculate an \( r^2 \) according to the formula

\[
r^2 = 1 - \frac{(\chi^2/N)/(SD^2)}
\]

where \( N \) is the total number of saccadic gains measured in an adaptation session and \( SD \) is the standard deviation of these gains.

All the 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 National Institutes of Health standards as stated in the Guide for the Care and Use of Laboratory Animals (Department of Health, Education and Welfare Publication NIH85-23, 1985) and recommendations from the Institute of Laboratory Animal Resources and the American Association for Accreditation of Laboratory Animal Care.

**RESULTS**

**Gain changes during adaptation**

**General features.** All four monkeys showed a decrease of saccadic gain (saccadic amplitude/initial target step amplitude) when subjected to the backward-jump adaptation paradigm and an increase of gain in the forward-jump paradigm. To illustrate the salient features of adaptation, Fig. 1 shows representative responses of monkey R, which was subjected to backward jumps during only rightward saccades on one day (Fig. 1A) and forward jumps during only leftward saccades on another (Fig. 1B). The earliest targeting saccades initiated in the backward-jump paradigm overshot the target and were followed by a backward corrective saccade (Fig. 1A2). Gradually, the initial saccade decreased in amplitude (Fig. 1A3) until, after several hundred responses in the adapted direction, this monkey’s initial saccade often went directly to the final target location and no corrective saccade was necessary (Fig. 1A4). Similarly, during adaptation with forward intrasaccadic jumps (Fig. 1B), saccades...
initially undershot the final target position and were followed by forward corrective saccades. In time, the initial saccade became larger so that, again after several hundred responses in the adapted direction, saccades often landed directly at the final target location.

To display the size and time course of the saccadic gain change, we plotted gain (HE/HT in Fig. 1) as a function of the number of the saccade made in the adapting direction. Figure 2 shows a plot of gains determined from all the saccadic responses to 5, 10, and 15° target steps during either the backward-jump (Fig. 2A) or forward-jump (Fig. 2B) paradigm in monkey R. As was typical for all four monkeys, the saccadic gain at neighboring times in the adaptation process was variable but, on average, it changed monotonically with the number of the adapted saccade. The trial-to-trial variability in gain did not appear to be related either to initial eye position or to whether the saccades were centrifugal or centripetal. To address whether the variability in gain was related to the initial position from which the saccade was launched, we compared the gains of adapted saccades of <10°, which began between 10 and 20° in the adapted direction (centrifugal saccades), with those beginning between 10 and 20° in the nonadapted direction (centripetal saccades). In two 50% backward-jump experiments each in monkeys A and R, there was no consistent difference in the average gains and variability of centrifugal and centripetal saccades. However, the state of gain adaptation did seem partially dependent on the monkey’s vigilance. If an adapted monkey stopped tracking and looked around the enclosure, the first few saccades after the monkey resumed tracking generally were not as well adapted.

To quantify the data of Fig. 2 with an objective metric that would allow comparison with existing studies, we fit the relation between gain and the number of the adapted saccade with an exponential function. From the exponential fit, we determined an asymptotic gain and a rate constant, when normal saccadic gain had changed by 63% of its asymptotic value. For the data in Fig. 2, the fits showed that backward adaptation reduced the gain to an asymptote of 0.69 with a rate constant of 608 saccades, whereas forward adaptation increased the gain to an asymptote of 1.25 with a rate constant of 678 saccades.

We assessed how well an exponential curve accounted for the gain data by two measures. First, because we continued to adapt the monkeys until their saccades observed on an oscilloscope apparently had reached a steady gain, we
FIG. 2. Saccadic gain as a function of when a saccade occurred in the adaptation sequence (i.e., its number) for a 30% backward-jump (A) and a 30% forward-jump (B) adaptation experiment followed by recovery in monkey R. Intrasaccadic adapting steps occurred only for initial target steps of 5, 10, and 15° to the left (●). Gains of the last 400 rightward (nonadapted) saccades appear near the end of adaptation in A and B (○). In the adapted direction, the gain data were fit with exponential functions with asymptotes (A), rate constants (C), and correlation coefficients ($r^2$) as shown in the insets. The large datum with error bars at the left of A and B represents the average gain (mean ± SD) in the adapted direction before adaptation (±100 preadapted saccades in each condition). Arrows: rapid gain change that accompanied the onset of recovery, which was produced by simple target steps in both directions.

could compare the measured gains of the last 100 adapted saccades with those predicted by the asymptotic gain fits. The similarities of the fitted and measured gains were different for backward and forward horizontal adaptation. After backward-jump adaptation, the asymptotic gain was the same as the measured gain for 15% jumps, 0.011 ± 0.020 (SD) lower than the measured gain for 30% jumps ($n = 18$), and 0.060 ± 0.045 lower for 50% jumps ($n = 11$). After the 30% forward-jump adaptation, however, asymptotic gain was 0.07 ± 0.056 higher than measured gain ($n = 11$). These data indicate that the exponential asymptotes are very representative of the actual gains at the end of adaptation for backward jumps to 30% but predict greater end adaptation gain changes for larger backward and all forward adaptations. In part, this discrepancy occurs because adaptation to 50% backward jumps and 30% forward jumps takes longer, as we shall see later, so the measured gains had not yet reached the asymptotic values. Second, the extent to which the exponential curves accounted for the data also was assessed by calculating the total variance, $r^2$ (see MATERIALS AND METHODS). The $r^2$ values also varied according to the percentage of the intrasaccadic target jump and whether it was backward or forward: $r^2$ averaged 0.15, 0.39 ± 0.15, and 0.50 ± 0.14, respectively, for 15, 30, and 50% backward adaptation, and 0.22 ± 0.17 for 30% forward adaptation (Table 1). These data indicate that exponential functions account for more of the variance in data obtained for backward than for forward gain changes and more of the variance in data obtained for larger than for smaller gain decreases.

On the basis of such exponential fits, we now demonstrate that the adaptation process varies for different adaptation conditions and different monkeys. Four monkeys served in a total of 45 different experiments. In the backward direction, they were subjected to horizontal intrasaccadic jumps of 15% ($n = 5$), 30% ($n = 12$), and 50% ($n = 11$) and vertical jumps of 30% ($n = 6$). In the forward direction, they were subjected to horizontal intrasaccadic jumps of 30% ($n = 11$).

THIRTY PERCENT BACKWARD-JUMP ADAPTATION. Figure 3 compares the course of gain reduction in response to 30% backward jumps in all 12 experiments performed with the four monkeys. The course of adaptation as measured by
30% Vertical Backward
Jump
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we adapted the saccades of monkeys S and A and a third subject, monkey M (used only for these experiments), to 30% backward jumps of one target size only and compared the gain changes of these adapted saccades with gain changes of saccades to target steps of other sizes. All post-adapted data were gathered during the gain recovery period with adapted target sizes interleaved with nonadapted target sizes. Following an average 17.3% reduction in gain of saccades to 15° target steps in monkeys A and M, the gain of saccades to 5° steps was reduced by an average of only 5.2%, yielding an average gain transfer of ~30% to the nonadapted saccade size (Fig. 4, top). After an average 17.4% reduction in gain of saccades to 5° target steps in monkeys A, M, and S, the gain of saccades to 15° steps was reduced by an average of 5.9%, yielding an average gain transfer of 34% (Fig. 4, middle). The transfer of adaptation improved as the size of the nonadapted target step approached that of the adapted step. After saccades to 10° target steps had undergone an average gain reduction of 15% in monkeys A, M, and S, there was an average transfer of gain to nonadapted saccades to 5 and 15° targets of 62 and 81%, respectively (Fig. 4, bottom). Therefore, in the monkey, gain changes produced for saccades to target steps of one size transfer only partially to saccades made to other

**FIG. 3.** Exponential fits of the relations of gain vs. saccade number for all of the 30% horizontal backward-jump experiments to show the variability in adaptation characteristics for individual animals and across all 4 animals. Initial target steps during adaptation were 5, 10, and 15°. Solid curves: adaptation to the right. Dashed curves: adaptation to the left. Uninterrupted part of each curve: range of the data set contributing to the fit. Further extension of the fit to ~2,000 saccades is shown as an interrupted line or dash.
TABLE 2. Comparison of asymptotic gain decreases and rate constants to 5, 10, and 15° target steps when all steps undergo simultaneous 30% backward jump adaptations

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Gain Decrease</th>
<th>Rate Constant</th>
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<td>5°</td>
<td>10°</td>
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Monkey A
- 8/4/94 (R) 0.20 0.21 0.13 54 44 82
- 11/1994 (R) 0.17 0.19 0.24 55 82 71

Monkey B
- 11/18/94 (R) 0.25 0.23 0.20 172 223 227
- 11/22/94 (R) 0.27 0.27 0.24 59 103 93

Monkey R
- 6/1993 (L) 0.30 0.31 0.30 268 261 122
- 1/21/94 (L) 0.24 0.27 0.27 122 88 94
- 4/9/93 (R) 0.22 0.21 0.18 112 110 89
- 1/1994 (R) 0.28 0.30 0.31 277 485 242

Across all 4 monkeys, there was no consistent difference in the amount or rate of adaptation at different target sizes. (R) and (L) indicate that gain reductions were only to the right or left, respectively.

When gain changes were considered separately for different-sized target steps in the 50% backward-jump paradigm, their characteristic features were similar. For monkeys A, B, and R, the gain changes of saccades to 15° steps could be either greater or less than those to 5° steps on different days. For monkey S, the gain changes at 15° were consistently greater by 16%, on average, than those at 5°. Average rate constants for 15° versus 5° steps were smaller for monkeys A and R, greater for monkey S, and the same for monkey B. As was the case for 30% backward jumps, there was no consistent difference in gain changes or rate constants for different step sizes across monkeys undergoing the 50% backward-jump paradigm. Consequently, we again conclude that simultaneous adaptation to target steps of different sizes produces comparable saccadic gain changes at each step size after roughly equal numbers of saccades at each step size.

**FIFTEEN PERCENT BACKWARD-JUMP ADAPTATION.** We have shown that larger imposed gain changes (e.g., 50%), on average, go less far to completion and require more saccades than do smaller ones (e.g., 30%). To expand these observations, we adapted monkey S three times and monkey A twice to 15% backward jumps. Both the average percentage of gain change and the rate constants were less for the 15% than for the 30% backward-jump paradigm (Table 1). These two monkeys changed their gains by 81% of the imposed backward jump during the 15% backward-jump paradigm versus 68% for the 30% paradigm and 58% for the 50% paradigm. The rate constants averaged across both monkeys increased with the required percentage of adaptation from 163 saccades for the 15% paradigm to 276 saccades for the 30% paradigm and 501 saccades for the 50% paradigm.

**THIRTY PERCENT VERTICAL BACKWARD-JUMP ADAPTATION.**

As was the case for 30% backward jumps, there was no consistent difference in gain changes or rate constants for vertical target steps when all steps undergo the 50% backward-jump paradigm. Consequently, we again conclude that simultaneous adaptation to target steps of different sizes produces comparable saccadic gain changes at each step size after roughly equal numbers of saccades at each step size.

**THIRTY PERCENT HORIZONTAL FORWARD-JUMP ADAPTATION.**

For the 11 forward-jump adaptation experiments, ≥2 in each animal, the magnitude of the percentage of gain increase averaged across all animals was comparable with the magnitude of the percentage of gain decrease caused by 30% backward-jump adaptation in either the horizontal or vertical directions (Table 1). Individual animals, however, showed either smaller or greater gain changes for forward than for backward adaptation. For monkeys S and B, which underwent multiple adaptation sessions, the large SDs indicate a considerable session-to-session variability.
in the number of saccades required for adaptation, similar to that described earlier for 30% backward-jump adaptation. In contrast, the average rate constants for all monkeys were always greater for 30% forward than for 30% backward jumps. Furthermore, the $r^2$ value (see METHODS) also was considerably greater for curves fitted to data from 30% horizontal backward-jump experiments than for curves fitted to forward-jump data (Table 1). Therefore, although the average percentage of gain change was similar in 30% forward- and backward-jump experiments, the process underlying gain increases seems fundamentally different from that underlying gain decreases of the same magnitude. Like 30% backward-jump adaptation, 30% forward-jump adaptation produced asymptotic gains that were similar for target steps of 5, 10, and 15°.

GAIN ADAPTATION IS DIRECTION SPECIFIC. In contrast to saccades in the adapted direction, saccades in the opposite direction showed no noticeable change in gain (Fig. 2, $\Delta$) during either backward- or forward-jump adaptation. As we
did for the adapted direction, we initially tried to fit gain changes in the opposite direction with an exponential curve. However, the gain changed so little that the fits often provided nonsensical data, e.g., rate constants that varied from several thousand to several million saccades. Therefore, to document that the gain in the opposite direction remained roughly constant throughout adaptation, we compared the average gain of the initial 50 saccades in that direction with the average gain of the 450th–500th saccades in those experiments that yielded sufficient data. In neither the 30% (n = 16) and 50% (n = 11) backward-jump adaptations nor the 30% (n = 11) forward-jump adaptation were the average gains of the earlier and later saccades in the opposite direction significantly different. Although the average rate constant for the 50% backward jumps and the 30% forward jumps in the adapted direction was >500 saccades (Table 1), we were obliged to use only 500 saccades in the opposite direction to include data from several experiments. Even in the 50% backward- and 30% forward-jump experiments, however, if there had been adaptation in the opposite direction with the same time course as that in the adapted direction, the gains after 500 saccades would have been significantly lower and higher, respectively, than the gains of the initial saccades.

Gain changes during recovery

GENERAL FEATURES. After a monkey had adapted to a stable gain, we sometimes required it to track simple target steps to induce saccades to recover toward their preadapted normal gains. We again fit the recovery data with an exponential curve to provide an asymptotic gain, a rate constant and a measure of variance. Because recovery, like adaptation, could require >2,000 total saccades, the monkey often quit working before it had completely recovered to its preadapted gain, as in the experiment shown in the Fig. 2B. Therefore we expected that the gain determined from the last 50–100 recovering saccades might not accurately reflect the asymptotic gain, and indeed that was the case. For recoveries after 15, 30, and 50% backward-jump experiments, the asymptotic gain was higher by 0.03 ± 0.02 (n = 5), 0.03 ± 0.03 (n = 8), and 0.09 ± 0.08 (n = 10), respectively; for recovery following the 30% forward-jump experiments, the asymptotic gain was lower by 0.02 ± 0.02 (n = 9). For recovery after 15, 30, and 50% backward-jump experiments, r² averaged 0.09 ± 0.05, 0.25 ± 0.11, and 0.37 ± 0.16, respectively; for recovery following 30% forward-jump experiments, r² averaged 0.19 ± 0.14 (Table 3). Therefore, on the basis of both the asymptotes and the r² values, the exponential fits accounted for less of the variability in the recovery data than in the adaptation data.

RAPID INITIAL RECOVERY. As can be seen in Fig. 2, there was an initial rapid change in gain at the onset of recovery. To quantify this change, we compared the asymptotic gain reached during adaptation with the y-intercept of the exponential fit to the recovery gain data (see Fig. 2). After the 30% horizontal backward-jump paradigm, the average initial recovery gains were higher by 0.07, 0.04, 0.02, and 0.01 (grand average: 0.035 ± 0.026) in monkeys R, S, B, and A, respectively. After 50% backward-jump experiments, the average initial rapid gain increase was 0.17, 0.05, 0.12, and 0.05 (grand average: 0.098 ± 0.058) in the same monkeys. For the two monkeys tested in the 15% backward-jump paradigm, the initial rapid gain increase was 0.01 and 0.02 in monkeys A and S, respectively. After 30% forward-jump adaptation, there was an initial rapid decrease in gain of 0.08, 0.08, 0.06, and 0.16 (grand average: 0.095 ± 0.044) for monkeys R, S, B, and A, respectively.

In some experiments there also was an initial rapid change in gain at the beginning of adaptation, but it was much smaller. We calculated the rapid initial gain change at the onset of adaptation as the difference between the preadapted gain and the intercept of the fitted adaptation gain curve. At the onset of 30 and 50% horizontal backward- and 30% forward-jump adaptations, the initial change in gain averaged a modest 0.01.

RECOVERY FROM LOW GAINS. After being subjected to a horizontal 30% backward-jump paradigm, monkeys R, S, and A each underwent at least two episodes of recovery (Table 3). These animals returned to an average asymptotic gain of 0.96 ± 0.015, which amounted to an average gain increase of 27.4 ± 6.7%. The average rate constant for recovery was 354 ± 90 saccades. After a vertical 30% backward-jump experiment, monkeys R, B, and A each experienced two episodes of recovery (Table 3). They exhibited an overall average gain increase of 21.9 ± 6.3% and an average rate constant of 421 ± 194 saccades. Each of the four monkeys experienced at least two episodes of horizontal 50% backward-jump adaptation followed by recovery (Table 3). Gain increased to an average asymptote of 1.02 ± 0.08, which amounted to an overall average percentage gain increase of 49.6 ± 19% and required an average rate constant of 711 ± 346 saccades.

RECOVERY FROM HIGH GAINS. After a 30% horizontal forward-jump episode, monkeys R, S, and B each underwent at least two sessions of recovery (Table 3). These animals decreased their average gain to an asymptotic value of 1.01 ± 0.06, an average percentage gain decrease of 18.0 ± 3.6%. Their average rate constant was 324 ± 109 saccades.

ADAPTATION ALSO AFFECTS THE GAIN OF CORRECTIVE SACCADES. During the early stages of recovery from low gains, the monkeys always made at least one forward corrective saccade to correct for the hypometria of the primary saccade. Immediately after a 50% backward-jump adaptation, responses to the earliest simple target steps during recovery usually elicited two and occasionally three corrective saccades, whereas before adaptation, dysmetria usually was corrected with only a single corrective saccade. The presence of multiple corrective saccades, which decreased in size as the target was approached, suggests that the corrective saccades also had undergone adaptation.

To quantify the amount of adaptation, we calculated the gain of the secondary saccade as the ratio of saccade size to the residual error, i.e., the difference between the target step and the size of the primary saccade. Figure 5 plots the gain of secondary saccades as a function of residual error after monkeys R (Fig. 5A) and A (Fig. 5B) had undergone a 50% backward-
jump adaptation. In *monkey R*, errors of less than ±2.5° resulted in saccades whose gains were quite variable, ranging from ±0.6 to 1.2. Although a few small saccades (≈17%) seemed to be at least partially adapted with gains of <0.8, the average gain for the entire population of secondary saccades responding to residual errors of ±2.5° (average ± 0.32°) was 0.92 ± 0.14. In contrast, the gain of secondary saccades to residual errors of ±2.5° (highlighted by the shading in Fig. 5) showed less variability and decreased with residual error. At errors of ±2°, the gain of secondary saccades, on average, was comparable with the average gain of primary (adapted) saccades to target steps (and therefore residual errors) of the same size (see mean and SDs in Fig. 5A). Therefore it appears that the secondary corrective saccades of *monkey R* also showed adaptation. The same general trends held for the more variable data from *monkey A* (Fig. 5B). Gains of secondary saccades correcting small residual errors (<2°) were quite variable. For larger errors (highlighted by shading), average gain decreased as a function of residual error. For *monkey A*, secondary saccades correcting ±2° residual errors had roughly the same average gain as primary (adapted) saccades to ±2° target steps, suggesting that this monkey also exhibited a substantial gain transfer from adapted primary saccades to secondary saccades.

The data in Fig. 5 indicate that adaptation of primary saccades to the ±2° target steps transferred poorly, if at all, to corrective, secondary saccades of <2–3°. One explanation might be that the gain changes of these smaller saccades were not demonstrable because small saccades readapted very rapidly. Alternatively, all types of smaller saccades may simply adapt poorly so that adaptation of primary ±2° saccades also would transfer poorly to smaller primary saccades. However, this expectation might be difficult to confirm in monkeys trained to our level of competence, because the spread of saccadic gains increased considerably for small saccades (Fig. 5).

We do not present data from 30% backward-jump adaptations because the residual error remaining after the hypometric saccades in that condition tended to be <3°, making it impossible to demonstrate the phenomena illustrated in Fig. 5.

### Long-term retention of gain decreases

We next asked whether the gain adaptation produced by this paradigm indeed reflects a "plastic" change in the nervous system by testing whether the gain changes endured if an adapted animal did not receive stimuli that promoted recovery. After all four animals had been adapted in the 30% horizontal backward-jump paradigm, we placed them in the dark for 20 h and measured the gain immediately thereafter. Saccadic gains for different-sized target steps before and after adaptation and after the animals had spent the next 20 h in the dark are shown in Fig. 6. As expected from the earlier data, backward-jump adaptation reduced saccadic gain to ±0.7–0.8 in all four monkeys. After 20 h in the dark, the saccadic gains were still adapted to an extent that varied considerably from animal to animal. In *monkey R*, the gains after 20 h were identical to those after adaptation, indicating a complete retention of the adapted gain. In the other monkeys, the gains after 20 h lay between adapted andpreadapted values, indicating a partial retention of gain. The least retention occurred for *monkey S*, whose smallest saccades had returned to normal gains after 20 h in the dark but whose larger saccades had gains that were still slightly

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**TABLE 5. Characteristics of saccadic gain recovery**

<table>
<thead>
<tr>
<th>Paradigm</th>
<th>Monkey</th>
<th>Number of Experiments</th>
<th>Actual Adaptation Gain</th>
<th>Asymptotic Recovery Gain</th>
<th>Percent Gain Change</th>
<th>$r^2$</th>
<th>Rate Constant</th>
</tr>
</thead>
<tbody>
<tr>
<td>After 30% Horizontal Backward Jump</td>
<td>R</td>
<td>2</td>
<td>0.72</td>
<td>0.97</td>
<td>35</td>
<td>0.39</td>
<td>457</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>3</td>
<td>0.77 ± 0.05</td>
<td>0.94 ± 0.06</td>
<td>22.2 ± 7.1</td>
<td>0.18 ± 0.08</td>
<td>292 ± 214</td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>2</td>
<td>0.78</td>
<td>0.97</td>
<td>25.2</td>
<td>0.21</td>
<td>313</td>
</tr>
<tr>
<td>Average across monkeys</td>
<td></td>
<td>0.76 ± 0.03</td>
<td>0.96 ± 0.02</td>
<td>27.5 ± 6.7</td>
<td>0.26 ± 0.11</td>
<td>354 ± 90</td>
<td></td>
</tr>
<tr>
<td>After 50% Horizontal Backward Jump</td>
<td>R</td>
<td>3</td>
<td>0.64 ± 0.06</td>
<td>1.13 ± 0.12</td>
<td>77.4 ± 1.8</td>
<td>0.56 ± 0.08</td>
<td>1,204 ± 163</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>2</td>
<td>0.73</td>
<td>0.99</td>
<td>36.9</td>
<td>0.20</td>
<td>691</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>2</td>
<td>0.69</td>
<td>0.95</td>
<td>38.8</td>
<td>0.33</td>
<td>429</td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>3</td>
<td>0.70 ± 0.04</td>
<td>1.02 ± 0.04</td>
<td>45.3 ± 11.2</td>
<td>0.33 ± 0.12</td>
<td>519 ± 220</td>
</tr>
<tr>
<td>Average across monkeys</td>
<td></td>
<td>0.69 ± 0.04</td>
<td>1.02 ± 0.08</td>
<td>49.6 ± 18.9</td>
<td>0.36 ± 0.15</td>
<td>711 ± 346</td>
<td></td>
</tr>
<tr>
<td>After 30% Vertical Backward Jump</td>
<td>R</td>
<td>2</td>
<td>0.74</td>
<td>0.92</td>
<td>23.8</td>
<td>0.32</td>
<td>334</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>2</td>
<td>0.78</td>
<td>0.89</td>
<td>14.9</td>
<td>0.13</td>
<td>286</td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>2</td>
<td>0.83</td>
<td>1.06</td>
<td>27.1</td>
<td>0.09</td>
<td>643</td>
</tr>
<tr>
<td>Average across monkeys</td>
<td></td>
<td>0.78 ± 0.05</td>
<td>0.96 ± 0.09</td>
<td>21.9 ± 6.3</td>
<td>0.18 ± 0.12</td>
<td>421 ± 194</td>
<td></td>
</tr>
<tr>
<td>After 30% Horizontal Forward Jump</td>
<td>R</td>
<td>2</td>
<td>1.22</td>
<td>0.95</td>
<td>-22.1</td>
<td>0.42</td>
<td>447</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>3</td>
<td>1.14 ± 0.05</td>
<td>1.01 ± 0.03</td>
<td>-15.4 ± 6.6</td>
<td>0.09 ± 0.02</td>
<td>241 ± 140</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>3</td>
<td>1.28</td>
<td>1.06 ± 0.02</td>
<td>-16.5 ± 3.8</td>
<td>0.18 ± 0.07</td>
<td>283 ± 52</td>
</tr>
<tr>
<td>Average across monkeys</td>
<td></td>
<td>1.21 ± 0.07</td>
<td>1.01 ± 0.06</td>
<td>-18.0 ± 3.6</td>
<td>0.23 ± 0.17</td>
<td>324 ± 109</td>
<td></td>
</tr>
</tbody>
</table>

*Values with ± are means ± SD. Percent gain change was calculated for each experiment and then averaged, and therefore may differ slightly from percentages calculated from the differences of average actual adapted and asymptotic gains. The actual adapted gain is the mean of the last 100 saccades of adaptation before recovery began.*
monkey A showed a decrease of gain both immediately after adaptation and 20 h later, monkey B showed an increase at both times, and monkeys R and S showed no differences after adaptation and 20 h later.

Effects of adaptation on saccadic metrics and latency

METRICS. Stepping the target backward during a saccade not only produced a gradual reduction in saccadic gain but also changed the metrics, i.e., duration and peak velocity, of some saccades in some monkeys (e.g., Fig. 1A4, dashed line). The affected saccades were both slower and of longer duration. The difference in saccadic metrics before and after monkey R had experienced a 50% backward-jump paradigm is shown in Fig. 7. The smallest adapted saccades (Fig. 7B) were about the same as preadapted saccades of roughly the same size (Fig. 7A), i.e., had similar position and velocity profiles. In contrast, larger adapted saccades (Fig. 7D) showed considerably more variability and were slower and of longer duration, on average, than preadapted normal saccades of about the same size (Fig. 7C). However, even some of the larger saccades had normal durations and peak velocities. Finally, the larger adapted saccades tended to have bigger vertical components than did normal saccades.

It is well known that a saccade’s peak velocity and duration depend on its size (Becker 1989). Therefore we assessed adaptation-induced changes in the saccadic metrics of monkeys A, B, and R by fitting curves to the peak velocity-versus-amplitude and duration-versus-amplitude relations and comparing the characteristics of the fitted functions (Figs. 8 and 9). We fit the peak velocity-versus-amplitude relations with a parabola, which was forced through zero peak velocity at zero amplitude, and the duration-versus-amplitude relations with a straight line as traditionally has been done for the so-called main sequence saccades (Becker 1989). This maneuver showed that adaptation had a large effect on saccadic metrics in monkey R (Fig. 8) but not in monkeys A and B (Fig. 9). Figure 8 shows how saccadic peak velocity (Fig. 8A) and duration (Fig. 8B) varied as a function of saccadic amplitude before and after monkey R underwent a 50% backward-jump adaptation (not the case illustrated in Fig. 7). Before adaptation, a quadratic function nicely described the increase of peak velocity with amplitude ($r^2 = 0.76$) but a straight line accounted for less of the variance in the duration-versus-amplitude relation ($r^2 = 0.40$). The high correlation coefficients before adaptation were due in part to the tight clustering of data points for saccades of approximately the same size, especially for movements of $<10^\circ$. After adaptation, the data showed more variability and many saccades were slower and lasted longer than those before adaptation. The slowing of postadapted saccades is clearly seen in the fitted curves for duration ($r^2 = 0.38$) and peak velocity ($r^2 = 0.38$). Postadapted saccades, on average, were slower than normal for all amplitudes, unlike the saccades illustrated in Fig. 7, which were slower only for larger amplitudes. The difference between pre- and postadapted saccades illustrated in Fig. 8 was among the most robust we observed.

On the basis of such fitted curves, monkey R exhibited

![Diagram of saccade gain and residual error](image_url)
FIG. 6. Retention of saccadic gain adaptation after 20 h in the dark. Saccadic gain as a function of saccadic amplitude before adaptation (×-×-×), after 30% imposed gain reduction (□ – □ – □), and after a subsequent 20 h in the dark (● – ● – ●). Adaptation was for 5, 10, and 15° initial target steps to the left for monkeys A and S and to the right for monkeys R and B. Monkeys R, B, and A retained at least some gain reduction at all saccadic amplitudes after their dark experience whereas monkey S retained only a modest gain reduction at large amplitudes. In the direction opposite to that adapted, there was no consistent gain reduction.

an average slowing of postadapted saccades of at least some sizes in all seven experiments performed with either the 30% (n = 4) or 50% horizontal backward-jump paradigm. The slowing was slightly greater for the 50% than for 30% backward-jump adaptations, and was generally greater for rightward than for leftward saccades in either paradigm.

In contrast to monkey R, the other three monkeys exhibited little, if any, slowing after backward-jump adaptation. Figure 9 shows representative data from monkeys A and B. Like the preadapted saccades of monkey R, those of monkey A were tightly clustered. Many of the adapted saccades had peak velocities and durations characteristic of preadapted saccades, but some were much slower and of longer duration than normal. Although these slower saccades were in a minority, they caused the fitted postadapted curves to be shifted slightly toward slower peak velocities and longer durations. In the three other experiments on monkey A, including two more 50% backward-jump adaptations, a modest slowing of saccades like that demonstrated in Fig. 9A was obtained in only one. The preadapted normal saccadic data from monkey B were more scattered (Fig. 9B) than those from monkeys R and A. As was the case for the other two monkeys, the postadaptation data of monkey B were quite variable. However, the fitted peak velocity- and duration-versus-amplitude relations after adaptation were essentially identical to those before adaptation. In a total of four experiments, including two with 50% backward-jump adaptation, both the fitted curves and the distribution of data points showed that monkey B had reduced saccadic velocity in only one of the 30% backward-jump experiments. Finally, in five experiments in monkey S, four requiring 30% and one requiring 50% backward-jump adaptation, only the 50% backward-jump adaptation was accompanied by saccadic slowing.

In summary, changes in saccadic metrics during gain reduction adaptation were inconsistent, occurring reliably in only one of the four monkeys. However, that animal, monkey R, consistently exhibited the largest gain de-
FIG. 7. Superimposed trajectories of 11–39 saccades before (A and C) and after (B and D) 50% backward-jump adaptation of saccades to small (A and B) and larger (C and D) target steps in monkey R. Traces, from top to bottom: horizontal eye position, vertical eye position (VE), horizontal eye velocity (HE), and vertical eye velocity (VE). Solid lines: averages of all responses. Although small saccades before and after adaptation were quite similar, larger adapted saccades tended to be slower and of longer duration.
FIG. 8. Peak saccadic velocity and duration as a function of saccadic amplitude before (Preadapted, ×–––×) and after a 50% backward-jump adaptation (Adapted, ⋄) and after a comparable number of saccades to simple target steps to test the effects of fatigue (Fatigue, −−−−). Duration-vs.-amplitude relations are fit with straight lines and peak velocity-vs.-amplitude relations with quadratic functions that have been forced through 0 amplitude and velocity. Values of $r^2$ for normal, adapted, and fatigue conditions were 0.76, 0.38, and 0.85, respectively, for peak velocity and 0.40, 0.38, and 0.70, respectively, for duration. Fatigue does not completely account for the slowing of adapted saccades. In this experiment, saccades to 5, 10, and 15° target steps were adapted in monkey R. This is a different experiment from that in Fig. 7.

creases of all four animals, suggesting that slowing may have facilitated, or been part of, its adaptation process. Indeed, as we were gathering the adaptation data it seemed that the saccades that landed closest to the back-jumped target often were unusually slow for all the monkeys. This observation can be documented by plotting saccadic gain versus peak saccadic velocity (Fig. 10). Before adaptation, the saccadic gain of monkey R was rather constant near 1.0 for saccades with peak velocities ranging from 200 to 800°/s ($\Delta$). After gain reduction produced by 50% backward-jump adaptation, saccades with the lowest gains had the lowest peak velocities. Similar trends were obtained in seven of the eight 50% backward-jump experiments across all four animals. Therefore in all monkeys saccades with the lowest adaptation-induced gains tended to exhibit the greatest reduction in velocity.

Saccadic slowing in monkey R not only occurred during the adaptation process but also persisted into recovery. Because this animal often made 1,000–2,000 saccades in the adapted direction before reaching a stable gain, slowing of adapted saccades might have been due simply to fatigue. To evaluate that possibility, we required the animal to make >5,000 total saccades to simple target steps in the adapted and opposite directions and compared the metrics of those "fatigued" saccades with the metrics of adapted saccades. In the experiment shown in Fig. 8, the fatigued saccades were slightly slower than those at the beginning of the experiment, but their slowness accounted for less than half of the slowing of adapted saccades. In seven experiments requiring either 30 or 50% backward-jump adaptation, fatigue accounted for about half to essentially all of the reduction in saccadic velocity.

Finally, we also examined the metrics of saccades after the 30% forward-jump paradigm in 11 experiments, with each of the four monkeys. Saccadic metrics, like gain, also were more variable during gain increases than
FIG. 9. Peak saccadic velocity and duration as a function of saccadic amplitude before gain reduction (x), after a 50% backward-jump adaptation (●), and after a comparable number of saccades to simple target steps to test the effects of fatigue (□) for monkeys A (left) and B (right). In these experiments, saccades to 5, 10, and 15° target steps were adapted. Values of r² for peak velocity/amplitude relations ranged from 0.65 to 0.81 for monkey A and from 0.41 to 0.74 for monkey B; values of r² for duration/amplitude ranged from 0.00 to 0.06 for monkey A and from 0.11 to 0.36 for monkey B. Fitted curves extend only over the range of the data.

FIG. 10. Saccadic gain as a function of peak eye velocity before (▲) and after (●) monkey R had experienced a 50% backward-jump adaptation. After adaptation, the slowest saccades tended to have the lowest gains.
decreases. On the basis of the fitted data points relating peak eye velocity or duration to saccadic amplitude, monkeys A and B exhibited convincing saccadic slowing, but the slowing appeared to be partly attributable to fatigue. Saccades after gain increases in monkeys R and S appeared to have normal metrics. Therefore, as was the case when adaptation produced gain reduction, we conclude that changes in saccadic metrics during gain increases are idiosyncratic from animal to animal. If changes do occur, they involve slowing, which seems to be due partly to fatigue associated with the apparently more arduous task of increasing saccadic gain.

Latency. It is possible that the neural events associated with saccadic adaptation require longer visual and/or motor processing, which might be reflected as increased latencies from the target step to the resulting saccade. To assess this possibility, we plotted the saccadic latency to the initial target step as a function of when the saccade occurred in the pre- to postadaptation sequence. We selected data from 50% backward-jump experiments because that paradigm produced the greatest saccadic slowing. For each monkey, we selected the experiment with the largest percentage of gain change (average of 40% reduction).

As with the slowing of adapted saccades, changes in reaction time also could be demonstrated for some monkeys but not for others. Monkey R exhibited a clear increase in saccadic latency, which was accomplished, in part, by elimination of saccades with very short, i.e., “express” (Fischer et al. 1984) latencies (Fig. 11, →). Average latency was significantly greater during adaptation (179 ± 44 ms) than before (135 ± 25 ms; P < 0.001) or after (158 ± 36 ms; P < 0.001) adaptation (Fig. 11, histograms). During recovery, saccades with express latencies returned. A similar situation occurred for monkey S (not shown), whose express saccades almost all disappeared ~20 min into adaptation. Average latency for this monkey was greater during adaptation (273 ± 145 ms) than before adaptation (198 ± 78 ms). Unlike monkey R, however, monkey S did not regain express saccades during recovery and saccadic latency did not decrease (311 ± 151 ms).

In contrast, adaptation was not accompanied by an increase in saccadic latency in monkey B (Fig. 11). Average saccadic latency during adaptation (200 ± 48 ms) did not differ significantly from the latencies either before (206 ± 60 ms; P < 0.42) or after (202 ± 50 ms; P < 0.58) adaptation (Fig. 11, histograms). Before adaptation, monkey B did not have a discernible subset of express saccades. Finally, monkey A, which also had no clear subset of express saccades before adaptation, did not exhibit latencies during adaptation that were significantly different from those either before adaptation (P < 0.11) or during recovery (P < 0.84).

Discussion

Our study shows that jumping a target forward or backward during a targeting saccade causes changes in saccadic gain, and these changes are appropriate to the size and direction of the step. However, the characteristics of this adaptation vary from monkey to monkey as revealed by substantial differences in the magnitude of the adaptation and its rate constant. Even the same monkey can exhibit quite different courses of adaptation when exposed to the same paradigm on different days. Part of the differences between animals might be attributable to the fact that they all did not undergo identical training regimens. In particular, monkey S was trained primarily to make accurate gaze shifts with head free, whereas the others were trained to make accurate eye saccades with heads fixed. Although monkey S showed the least adaptation and the poorest retention of adaptation after 20 h, it, like all the monkeys, showed some saccadic gain adaptation regardless of training history. Therefore we conclude that the gain adaptation elicited by the intrasaccadic target step paradigm is a ubiquitous phenomenon, which requires only that animals be able to follow a jumping spot.

Primate saccadic gain adaptation is not “parametric”

In a linear control system, alteration of the gain of an element in the forward pathway linking a stimulus to a response causes a proportionate change in the response to stimuli of all sizes. Our adaptation paradigm did not produce such a parametric gain change in the control system that produces a saccade. We know this because adaptation restricted to target steps of one size produced a substantial change in gain of saccades to that target step but smaller changes to target steps of other sizes (Fig. 4). For example, when saccades to targets stepping by 15° were adapted by backward jumps to produce an average 17.3% reduction of gain, there was only a 5.2% reduction in gain of saccades to 5° target steps (Fig. 4). Similarly, adapting saccades to 5° targets, which produced an average gain reduction of 17.4%, caused only a 5.9% reduction in saccadic gain to 15° target steps. Also, after adaptation had reduced the gain of primary saccades to 5° targets, no gain reduction occurred for smaller corrective saccades. Although the gain changes of adapted primary saccades to 5° targets were comparable with those of corrective saccades to 5° residual errors, small secondary saccades to residual errors of <2–3° showed little, if any, adaptation (Fig. 5).

Most studies of human saccades also have concluded that adaptation is not parametric. When saccades to one target size were adapted and saccades to target steps that were 50% greater and smaller were tested, only a 42% transfer from the adapted to the tested sizes occurred (Miller et al. 1981). In another study, saccadic adaptation to a target jumping to 21° produced <75% transfer to targets jumping to 14 and 28° and considerably less transfer to targets landing at 7 and 35° (Frens and van Opstal 1994). These authors concluded that adaptation is confined to a limited range of saccadic vectors around the oculocentric coordinates of the adaptation target, which they called a “restricted adaptation field.” Others have shown similar partial transfer in gain from adapted saccades to larger and smaller tested saccades (Semmlow et al. 1989).

In contrast, Deubel et al. (1986) concluded that a 33.3% gain reduction of saccades to 12° target steps caused the same gain reduction of saccades to targets of 8 and 15°. A close examination of their data on humans in the context of our data on monkeys suggests that our data are not really in conflict with theirs. First, according to their Fig.
FIG. 11. Saccadic latency from the initial target step before (△) and during (●) adaptation and during recovery (○) as a function of time into the experiment. Representative sessions from monkeys R and B. During adaptation, the latencies of monkey R became longer and more variable; all express saccade latencies (→) disappeared during adaptation and reappeared thereafter. During adaptation, latencies for monkey B were unchanged. The 2 pauses in the data are brief periods when monkey B did not track the jumping target. For both monkeys, average latencies of saccades before adaptation (Pre), during adaptation (Adapt), and after adaptation (Recovery) are shown in histograms.

6, two of their four subjects did show slightly larger undershoots (i.e., lower gains) for adapted saccades than for larger or smaller tested saccades. Also, in our monkeys, the amount of transfer increased as the size of the tested saccade became more nearly equal to the size of the adapted saccade. Saccades to target steps with sizes within 5° of the adapted target step exhibited between ~60 and 80% gain transfer, on average (Fig. 4, bottom). Thus we suggest that if Deubel et al. had tested saccades more different in size from the adapted ones, they too would have found incomplete gain transfer.

The available evidence therefore favors the conclusion that the intrasaccadic adaptation paradigm does not produce a parametric gain change in any primate species. Rather, the best adaptation occurs for the condition that is adapted. This was demonstrated most graphically in experiments in which it apparently was possible in some human subjects to increase the gain of small saccades and simultaneously de-
crease the gain of large saccades in the same direction (Miller et al. 1981). Adaptation is specific not only to the size of the adapted saccade but also to its direction in both humans (Frens and van Opstal 1994) and monkeys (Deubel 1987). In monkeys, saccades tested at angles as little as 30° from the adapted direction showed little change in gain (Deubel 1987). That adaptation is specific to the size and direction of the adapted saccade should come as no surprise. Similar selective adaptation occurs for the vestibuloocular reflex, where forced rotation at one frequency to produce adaptation produces a gain change that does not transfer completely to other frequencies (Lisberger et al. 1983).

The finding that saccadic gain adaptation is specific to the size of the adapted saccade, i.e., that there is an adaptation movement field (Frens and van Opstal 1994), could have two simple explanations. First, adaptation could cause a remapping of the neural representation of a localized area on the retina on which the target step of a single size consistently falls. This would be considered a sensory-induced change in saccadic gain. Alternatively, the visual map could remain unaffected and adaptation could occur in the motor portion of the saccadic pathway. Experiments are currently under way to test whether saccadic gain adaptation is a sensory phenomenon, a motor phenomenon, or some combination of both.

Even though our paradigm strictly speaking does not produce a parametric gain change, our results suggest that it can be used to simulate one. First, we showed that the simultaneous adaptation of 5, 10, and 15° target steps produces similar gain changes for all three step sizes (Table 2). Second, saccadic gain changes due to single adapting steps transfer substantially to saccades elicited to step sizes within 5° of the adapting step. Therefore, by adapting saccades every 5° from 5 to 25°, we could produce a uniform gain change over the normal horizontal operating range of saccades with the head stationary. A uniform gain change for all size saccades is, of course, what would be expected to occur in most real-life situations, where it would be appropriate for movements of all sizes to recover because all had been compromised.

What signal drives the gain change?

LARGE OR SMALL ERRORS? We may gain some insight into the mechanisms that drive saccadic gain changes by comparing the characteristics of gain increases and decreases. We have three measures with which to compare adaptation produced by different conditions: the actual gain change accomplished, the number of saccades required to accomplish it as reflected by the rate constant, and the variability of the exponential course of the adaptation as reflected in values of r^2. Averages of these three values sorted for the different adaptation conditions are presented in Figs. 12 and 13 for our four monkeys.

With two exceptions in the data of *monkey R*, the actual gain change produced by adaptation was less than or equal to the imposed change (Fig. 12A). The larger the imposed gain change, the less the actual gain change went to completion. For the two animals tested in all conditions (*monkeys A* and *S*) the gain change was 81% complete for 15% backward jumps, 68% complete for 30% backward jumps, and only 58% complete for 50% backward jumps. This finding implies that there is a limit (a soft saturation in the data of Fig. 12A) to the gain changes that the adaptive mechanism can accomplish.

Recovery also required either increases or decreases in gain, which might engage the same mechanism that governs the gain increases and decreases that occur during adaptation. According to the data in Fig. 12A, the actual gain change seemed similar whether the imposed gain change was associated with adaptation (○, △, ●, ■) or with recovery (○, △, ○, □).

The observation that larger percentage gain changes went less to completion than smaller ones suggests that the adaptive mechanism might be limited by, and possibly driven by, the amount of the error that must be corrected after a dysmetric saccade. In our paradigm, as the imposed percentage gain change increased, so too did the error. For example, for a 15% backward jump, the saccadic error at the onset of adaptation ranged from 0.75 to 2.25° for 5 and 15° target steps, whereas for a 50% backward jump the error ranged from 2.5 to 7.5°. Perhaps the finding that small imposed percentage gain changes went more nearly to completion reflects an inability of the adaptation mechanism to deal with large errors. If this were true, however, the actual percentage gain changes produced by 50% backward jumps for 5° target steps (an initial 2.5° error) presumably would be larger than those for 15° steps (an initial 7.5° error). However, when we considered the gain changes that 50% backward-jump adaptation produced in saccades to 5 and 15° target steps separately, they were similar.

Another interpretation of our data is that the adaptation mechanism simply is limited in the range of gains it can achieve. To determine which factors limit the gain change, future animals could be adapted with forward or backward jumps of different fixed sizes, rather than with fixed percentage jumps as we have done here.

It makes good sense that the adaptation mechanism engaged by our behavioral paradigm is more efficient at correcting small errors or at affecting small gain changes. We imagine that, in real life, the adaptive mechanism is usually called on to correct rather small errors produced by gradual deterioration of a neural network. For example, normal aging, which undoubtedly is associated with modest, gradual cell loss, appears to have little effect on saccadic accuracy until the age of ~70 in humans (Hotson and Steinke 1988; Warabi et al. 1984). During aging, then, saccadic gain is well regulated. In contrast, when a patient has a catastrophic insult that causes a large dysmetria as occurs in Wallenberg’s patients and patients with ischemia of the rostral cerebellum, the saccadic adaptive mechanism is often unable to restore saccadic gain to normal and a small conjugate dysmetria persists (Straube, personal observations).

DOES ADAPTATION FAVOR GAIN INCREASES OR DECREASES? Several features of the data in Figs. 12 and 13 suggest that the adaptive mechanism has more predictable characteristics when it deals with gain decreases than when it deals with gain increases. First, the rate constants for a given percentage of gain decrease were quite similar whether the gain decrease...
FIG. 12. Characteristics of the gain adaptation process. Each datum represents the average of all the experiments performed in that condition on that animal. A: actual gain changes produced by different-sized imposed gain changes during adaptation ( ● , ▲ , ◆ ) and recovery ( ○ , △ , □ , □ ). The line of slope 1 indicates where data should fall if the actual gain change equaled the imposed gain change. Imposed gain changes were either ±15, 30, or 50%, but some data have been displaced slightly along the abscissa for ease of viewing. B: r² value of the exponential fits of gain vs. saccade number as a function of the actual percentage of gain change achieved in different adaptation and recovery experiments. A linear fit for gain decreases is a better (r² = 0.80) representation of the data than a linear fit of gain increases (r² = 0.50).

was the result of adaptation or recovery. Second, there was a tight linear relation between the rate constant and the actual percentage of gain decrease (r² = 0.92; when r² is in italics, we refer to a linear correlation). In contrast, the rate constants for increases in gain were quite variable for a given percentage of change and were poorly correlated with the percentage of gain increase (r² = 0.05). For example, the rate constants varied from 290 to >1,660 for actual gain increases between 22 and 26% (Fig. 13). Furthermore, gain increases required more saccades than did gain decreases, just as in humans (Deubel et al. 1986; Miller et al. 1981). Third, once we conclude that the course of gain change is best fit with an exponential function, the goodness of the exponential fit as revealed by r² indicates how variable the adaptation process is. On the basis of the value of r² (Fig. 12B), the exponential fit for a particular actual gain change (e.g., 40%) was better if it was a decrease (r² ~ 0.6) than an increase (r² ~ 0.3). Last, the initial rapid recovery of gain is larger after 30% forward than 30% backward adaptation experiments, suggesting that increased gain states might be less secure than decreased ones. Altogether, therefore, the process underlying a fall in gain appears to be far less variable than that underlying a rise, so that saccadic gain adaptation seems to employ a more coherent strategy when dealing with gain decreases than with gain increases.

Our suggestion that mechanisms for increasing saccadic gain are less well established than those for decreasing it depends, in part, on the wide range of rate constants for actual gain increases of 20–30% (Fig. 13). In many of those experiments, the gain increase occurred during forward adaptation ( ● , ▲ , ◆ ), which takes the gain away from its normal value near 1. However, if we conclude that the characteristics of gain adaptation might be most predictable when adaptation is returning saccadic gain to normal gain whereas those during recovery are toward normal gain. We believe these data, taken together, suggest that the mechanism that controls saccadic amplitude is best suited to drive gain downward because the characteristics of adaptation associated with gain decreases are more stereotyped than those accompanying gain increases. What are the implications of this observation? An efficient mecha-
nism for producing gain decreases would be especially useful if damage to the saccadic system usually produced a hypermetria, which would require gain reduction. However, hypermetria is a rather rare occurrence in the clinic, apparently occurring only after lesions to the cerebellum or its efferent and afferent pathways (D. Zee and A. Straube, personal communications). Another possibility is that the saccadic system prefers to undershoot the target and continually adjusts saccadic gain to do so. In this scenario, consistent undershooting could minimize either saccadic flight time (Harris 1995), expenditure of muscular energy, or programming time, because successive saccades in the same direction do not require switching from one side of the brain to the other (Robinson 1973). Undershooting indeed appears to be a deliberate strategy, because it is gradually restored if it is eliminated by optical devices that, like our paradigm, effectively shift a target backward during a primary saccade (Henson 1978). Because an undershooting mechanism already is in place, it could easily be mobilized when gain decreases are required.

Is there a role for changes of saccadic metrics in the adaptation process?

Reductions in saccadic gain seem to be accompanied by changes in saccadic metrics in some monkeys but not in others. Only monkey R showed convincing decreases in average peak velocity and increases in average duration for most saccades. Fatigue did not account entirely for the slowing. Although the adapted saccades of the other three monkeys were not slower, on average, even those monkeys made some saccades that were slower than preadaptation saccades of the same size. Furthermore, saccades that landed closest to the backward-jumped target location, i.e., had the lowest gain, tended to have slower velocities than normal (e.g., Fig. 10) in all monkeys. Such data suggest that saccadic slowing may be part of the mechanism associated with gain reduction. The ability of some monkeys to employ saccadic slowing may be correlated with the maximum amount of adaptation that can be attained; monkey R, which exhibited consistent slowing, also underwent the largest gain reductions of all the monkeys (Fig. 12A). More monkeys would need to be examined to determine whether this proposal has merit.

There is considerable controversy in the literature as to whether primates exhibit saccadic slowing during adaptation. In the only other monkey study we are aware of, saccades of $\sim 18^\circ$ in at least one animal had slower peak velocities after reductions in saccadic gain (Fitzgibbon et al. 1986). In humans, measurement of peak saccadic velocities (Albano and King 1989; Frens and van Opstal 1994), duration, and the skewness of the velocity profile (Frens and van Opstal 1994) revealed that gain reduction was accompanied by saccades with metrics in the normal range. In other studies on humans, however, backward adaptation caused standard $12^\circ$ saccades to have longer durations (but not lower peak velocities) than normal (Straube and Deubel 1995) and saccades of $\sim 7^\circ$ to have longer durations (Abrams et al. 1992). The discrepancy between these studies may be reconciled by our finding that some adapted monkeys (and therefore, probably some adapted humans) exhibit a clear change of metrics, whereas others do not.
Is adaptation of saccadic amplitude in monkeys different from that in humans?

The characteristics of adaptation produced by the intrasaccadic target jump paradigm differ in monkeys and humans. In particular, the time course of adaptation appears to be shorter for humans than for monkeys. This comparison is complicated because some investigators have adapted saccades to single target steps whereas others have used multiple steps, and adaptation with the use of a single target step is more rapid (Miller et al. 1981). If we concentrate only on human experiments in which saccades to multiple target steps were adapted, 25–30% backward jumps produced an asymptotic gain reduction in ~300–400 trials (a rate constant of ~100–133 saccades) in one study (Straube and Deubel 1995) and an average rate constant of 57 saccades in another (Miller et al. 1981). In contrast, the average rate constant for 30% backward jumps in our experiments averaged ~370 saccades (Table 1). Although it is possible that the differences in time course are caused by different adaptation processes, we favor the view that both species use the same mechanism but that it simply is faster in humans.

Do these differences in the characteristics of adaptation in humans and monkeys indicate that the monkey is not a good model for studying saccadic adaptation in humans? It is possible that humans adapt faster because they use a strategic component. Although this possibility cannot be discounted, it appears that a significant part of the human adaptive process does involve true plasticity, because humans apparently still show evidence of adaptation the day after the experiment (Deubel 1995), just as our monkeys did (Fig. 6). It would be desirable to quantify the retention of gain in humans by requiring adapted humans to remain in the dark for ≥12 h.

Changes in saccadic gain involve plastic changes in the brain

In the monkey, the process of saccadic gain change in the intrasaccadic target jump paradigm has two components. After adaptation, all animals displayed an initial rapid recovery of gain, whether recovery involved an increase or a decrease in gain. The rapid gain recovery averaged ~0.06 over all conditions and monkeys. Two of four monkeys also exhibited consistent rapid changes at the onset of adaptation, but these changes were much smaller. Because the initial gain changes at the onsets of adaptation and recovery were demonstrable within several trials, we suggest that these initial rapid, but small, changes were probably strategic.

On the other hand, we conclude that the subsequent gradual gain change during both adaptation and recovery (Fig. 2) is probably not strategic because of its slow time course. Furthermore, once gain was reduced by the 30% backward-jump paradigm, it remained reduced after the animal had spent 20 h in complete darkness (Fig. 6). The amount of gain reduction that was retained varied from complete for saccades of all sizes in monkey R to partial for saccades of >8° in monkey S. Substantial but not complete gain reduction was retained for the other two monkeys. These data suggest that the gradual decreases in gain are accomplished by true plastic renovations in the brain and that these alterations remain as long as the saccadic system is unaware that its saccades are hypometric.

It is unclear why the amount of gain retention after 20 h of darkness should have been so variable across monkeys. In real life, the demanded gain changes undoubtedly are smaller than the 30% changes required in these experiments. Furthermore, with repeated use an adaptive mechanism would have the opportunity to consolidate the changes. Therefore, if the animals had been adapted every day for several weeks and otherwise placed in the dark, the retention probably would have been more robust. We are unable to explain the poor retention in monkey S. However, this monkey generally was the worst adapter of all, displaying the lowest percentage of adaptation to both 30 and 50% backward jumps.

In conclusion, the intrasaccadic target step paradigm produces saccadic gain changes that are specific to the adapting conditions and are enduring. We believe these characteristics are the defining features of a mechanism that resists to some sort of neuronal reorganization or plasticity. Moreover, substantial plastic changes in saccadic gains can be induced within 1,000 trials. Because only 0.5–1 h is required to accumulate this number of trials, we are optimistic that this paradigm will allow us to record from saccade-related neurons while gain changes are actually taking place.

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