Saccadic Gain Modification: Visual Error Drives Motor Adaptation

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Wallman, Josh and Albert F. Fuchs. Saccadic gain modification: visual error drives motor adaptation. J. Neurophysiol. 80: 2405–2416, 1998. The brain maintains the accuracy of saccadic eye movements by adjusting saccadic amplitude relative to the target distance (i.e., saccade gain) on the basis of the performance of recent saccades. If an experimenter surreptitiously moves the target backward during each saccade, thereby causing the eyes to land beyond their targets, saccades undergo a gradual gain reduction. The error signal driving this conventional saccadic gain adaptation could be either visual (the post-saccadic distance of the target from the fovea) or motoric (the direction and size of the corrective saccade that brings the eye onto the back-stepped target). Similarly, the adaptation itself might be a motor adjustment (change in the size of saccade for a given perceived target distance) or a visual remapping (change in the perceived target distance). We studied these possibilities in experiments both with rhesus macaques and with humans. To test whether the error signal is motoric, we used a paradigm devised by Heiner Deubel. The Deubel paradigm differed from the conventional adaptation paradigm in that the backward step that occurred during the saccade was brief, and the target then returned to its original displaced location. This ploy replaced most of the usual backward corrective saccades with forward ones. Nevertheless, saccadic gain gradually decreased over hundreds of trials. Therefore, we conclude that the direction of saccadic gain adaptation is not determined by the direction of corrective saccades. To test whether gain adaptation is a manifestation of a static visual remapping, we decreased the gain of 10° horizontal saccades by conventional adaptation and then tested the gain to targets appearing at retinal locations unused during adaptation. To make the target appear in such “virgin territory,” we had it jump first vertically and then 10° horizontally: both jumps were completed and the target spot extinguished before saccades were made sequentially to the remembered target locations. Conventional adaptation decreased the gain of the second, horizontal saccade even though the target was in a nonadapted retinal location. In contrast, the horizontal component of oblique saccades made directly to the same virgin location showed much less gain decrease, suggesting that the adaptation is specific to saccade direction rather than to target location. Thus visual remapping cannot account for the entire reduction of saccadic gain. We conclude that saccadic gain adaptation involves an error signal that is primarily visual, not motor, but that the adaptation itself is primarily motor, not visual.

INTRODUCTION

Saccades are rapid, voluntary changes of gaze, usually to objects that attract one’s attention. Because saccades are very rapid [a 10° saccade lasts only ~50 ms and has a peak velocity of >500°/s (Becker 1989)] and visual processing in the retina is quite slow (latencies of ~30 ms at the optic tract), most saccadic movements are not visually guided. Instead, the accuracy of saccades is maintained by adjusting their amplitude relative to the distance of targets from the fovea. Such adjustments correct consistent tendencies of saccades to overshoot or undershoot their targets. The existence of this adaptive control of saccade amplitude has been inferred from many experiments during the past 30 years. In a typical experiment, the target is moved surreptitiously during a saccade (a period during which vision is poor because the eyes are moving so fast) so that a saccade that was in fact accurate appears to have been too large or too small. Over the course of many such deceptions, the average size of the saccade is adjusted so that the eye lands near the new target location (e.g., Deubel 1987; Deubel et al. 1986; McLaughlin 1967; Straube et al. 1997).

This adaptive plasticity can be viewed most simply as a parametric adjustment of a motoric gain, perhaps used in daily life to compensate for gradual changes in muscle efficacy or eye size. However, saccadic gain adjustment in humans seems too complex for so simple a mechanism. Saccadic gain can be adapted independently for different directions of movement [e.g., rightward saccades increased while leftward ones decreased (Semmlow et al. 1989)], for different amplitudes [e.g., 5° saccades increased while 20° saccades decreased (Miller et al. 1981)] and for different behavioral situations [e.g., visually triggered saccades increased without affecting memory-guided saccades or free-scanning saccades (Deubel 1995a,b; Erkelens and Hulleman 1993)].

Like humans, nonhuman primates show saccadic gain adaptation that is specific to particular directions and amplitudes. However, saccadic gain changes more slowly in monkeys than in humans (Albanese and King 1989; Straube et al. 1997), and the gain changes produced by adaptation of visually triggered saccades do transfer to scanning and memory-guided saccades (Fuchs et al. 1996).

We ask two independent questions about the saccadic gain adjustment of humans and monkeys: Is the adaptation a consequence of a change in a motoric gain or can it be explained as a static sensory remapping of the visual field? Regardless of whether the adaptation is visual or motoric, what kind of error signal drives adaptation?

To consider the second question first, the most obvious error signal would be the distance of the target from the fovea (retinal error) at the end of the saccade. Whereas such a signal would be easy to extract in the reduced laboratory situation of a single target spot in a dark room, it might be ambiguous in the case of spontaneous saccades in a normal environment with numerous potential targets present. If, after a saccade, there were stimuli on either side of the fovea,
the gain-control mechanism would need to know which stimulus had been the saccade target to know whether the saccade had overshot or undershot the target.

An alternative solution would be to use a motoric error signal, such as the direction of the small corrective saccades that follow inaccurate saccades. If the corrective saccade were in the same direction as the primary saccade it would signal that the saccadic gain needed to be increased and if in the opposite direction, that the gain needed to be decreased (Alban and King 1989). In this paper, we argue that the error signal for saccadic adaptation is not primarily a motoric one by showing that we can decrease saccadic gain whether corrective saccades are in the same direction as the primary saccade or in the opposite direction.

Whatever error signal is employed by the adaptation mechanism, the saccadic alteration itself could be either motoric or visual in origin. Because saccadic gain represents the relation between the perceived distance of the target from the fovea and the magnitude of the saccade to match that distance, a position error after a saccade could be interpreted in one of two ways. Either the perceived target distance is veridical and the saccade size needs adjustment or the saccade size is veridical and the perceived target distance needs adjustment. We explored these possibilities by assessing whether adaptation of saccades to targets in a small region of the visual field transfers to identical saccades made to targets in other regions of the visual field.

**METHODS**

**General procedures**

The subjects were five juvenile rhesus macaques (Macaca mulatta) and two adult humans who were experienced in oculomotor experiments. In the experiments on monkeys, eye movements were measured with the search coil technique, which measures the orientation of a coil affixed to the eye within surrounding alternating magnetic fields in spatial and temporal quadrature (Fuchs and Robinson 1966; Robinson 1963). For details about the surgery to implant the eye coil and the head restraints, see Fuchs et al. (1996). The monkeys were trained to follow a jumping target spot and were rewarded with applesauce if their eyes remained continuously within a certain distance (usually ±2°) of the target for several seconds. (This requirement was relaxed briefly when the target moved.) After 2±3 mo of training, the animals followed the jumping spot diligently over a ±20° range for several thousand trials each day.

In the experiments on humans, eye movements were measured not by search coils but by a photoelectric transducer, which detected differential reflections from the nasal and temporal iris-sclera borders along a horizontal line. The subjects’ heads were stabilized by a bite bar and forehead rest; the transducer position was adjusted to achieve a linear response over the ±20° range. Because this transducer was less stable than the eye coils, we did not rely on the initial calibration for assessing saccadic gain changes. Instead, we assumed that the subjects had been fixating the target accurately at the start of each trial and that their eyes maintained accurate fixation within 1±2 s after the target moved, by which time they had made no further corrective saccades. We regarded the overall change in eye position over this period as equal to the change in target position and used this measure as an internal calibration within each trial. The size of the initial saccade was expressed as a proportion of this total change.

For all experiments, the subjects were seated in a darkened room and targets were projected onto a tangent screen 67 cm in front of the subject or onto a drum 48 cm in front of the subject. The target was a red laser light spot, which subtended either 0.25 or 0.4° and was reflected off two mirror galvanometers situated orthogonal to each other. Voltages specified by a Macintosh IIx computer were applied to the galvanometers to produce target motion in two dimensions.

**Experimental protocols**

**CONVENTIONAL ADAPTATION.** Before each experiment, we collected 100±200 unadapted saccades as a measure of the subject’s normal saccadic gain. To do this, the spot stepped left or right randomly by either 7 or 10°, thereby landing at a variety of horizontal locations across the screen. During conventional adaptation, the same random target motion was used, except that during the saccade to each target step, the computer stepped the target back by either 30 or 40% of the original target step. The occurrence of a saccade was detected when eye velocity, as measured by analogue differentiation of eye position, exceeded ±50°/s. For 10° saccades, the backstep occurred ~10 ms before peak eye velocity. When we judged that horizontal saccades had reached a stable reduced gain after several hundred trials, we stopped the adaptation paradigm and tested the subject with ~30 simple target steps (except in the case of the virgin territory experiments described later in METHODS).

**DEUBEL BRIEF BACKSTEP ADAPTATION.** To produce saccadic gain decreases with few backward corrective saccades, we used an adaptation paradigm suggested by Heiner Deubel at the University of Munich. In this paradigm, as in conventional adaptation, when the eye makes a saccade in response to a target step, the target jumps backward by 30% of its initial step (40% in a few cases). In contrast to the conventional adaptation paradigm, the target dwells in the back-stepped location only briefly before returning to the location it had after its initial step; this return nearly always occurs before the occurrence of any corrective saccade. Examples of the target and eye movements elicited in this paradigm are shown in Fig. 1.

For each subject, the amount of time that the target dwelled in its back-stepped location was adjusted to be as long as possible without eliciting many backward corrective saccades. We employed this strategy because we reasoned that longer dwell times were more likely to facilitate saccadic gain adaptation. We had the impression that the expectation that the target would return to its previous location after the backstep produced a substantial increase in the saccadic reaction time. Therefore, we started each subject with relatively brief dwell times and then, once or twice during each experiment, we increased the dwell time as much as possible without causing the subject to make backward corrective saccades. The dwell times used for the monkeys were 117±200 ms at the onset of a session and increased to 183±283 ms by the end. For the human subjects, we used dwell times of 200±300 ms.

Monkeys and humans were subjected to the Deubel paradigm while they executed saccades to target steps in both the leftward and rightward directions; 80% of the steps were 10° and 20° were 7°. The function of the 7° target steps (which were not considered in the data analyzed) was to prevent the target from landing repeatedly at only a few locations. As with the conventional adaptation paradigm, after Deubel adaptation, we tested the subjects with ~30 simple target steps.

**CONVENTIONAL ADAPTATION TESTED BY DOUBLE STEPS IN VIRGIN TERRITORY.** To assess whether the saccadic adaptation could be localized to a definitively visual or motor level of neural processing, we attempted to disambiguate the two by testing whether adaptation was specific to the retinal location of the target step during adaptation or to saccades of the size and direction adapted. This was done in two stages. First we decreased the gain of purely horizontal saccades to 10 and 7° target steps by using conventional adaptation. Then we tested the adaptation of hori-
horizontal saccades to target steps of the same size as during adaptation but at a different retinal location, i.e., in virgin territory. We did this by requiring the eye to make first a vertical then a horizontal 10° saccade, starting with the eye and target straight ahead. To elicit this pair of eye movements, the target moved randomly either up or down and then, after a delay, randomly either to the right or left. The delay between the vertical and horizontal steps was adjusted to be just under the subject’s saccadic reaction time so the target appeared in its second location before the eye had begun to move. As the eye began its vertical saccade, its movement was detected at a velocity threshold of ~50°/s and the target spot was extinguished. Therefore, both the vertical saccade and the subsequent horizontal saccade were executed in complete darkness. After a 200- to 300-ms interval to ensure that both saccades had occurred, the target spot was turned on again and the monkey made a corrective saccade to the target. After the animal had been fixating the target accurately for ~1.5 s, the target jumped back to the starting position and, after a variable delay, the next trial began. These double-step trials were interleaved randomly with purely horizontal target steps so that the gain of the adapted saccades to simple horizontal steps and to the horizontal saccade of the double step could be measured simultaneously.

Monkeys found this double-step memory-guided saccade task to be quite difficult. During training, they were rewarded only when they executed first a vertical and then a horizontal saccade, and double-step trials were interleaved randomly with catch trials of purely vertical saccades. Despite these precautions, even cooperative monkeys followed both steps on only about three-quarters of the trials. On the other trials, they went directly to the eccentric target location with a single oblique saccade.

CONVENTIONAL ADAPTATION TESTED BY SINGLE OBLIQUE STEPS IN VIRGIN TERRITORY. To test whether the transfer of adaptation found on the double-step virgin territory experiment was specific to the retinal location of the target or to the direction of the saccade used to reach the target, we tested the adaptation of saccades to virgin territories in a second way. In this experiment, we decreased the gain of horizontal saccades by means of conventional adaptation and then required the monkeys to saccade to the same virgin territory loci used in the previous double-step experiments, but this time with a single oblique saccade. The monkeys were rewarded for tracking targets that moved either horizontally or obliquely at angles of ±22.5° and ±45° from horizontal to either the right or left. The horizontal component of all oblique target steps was kept at 10°. Starting at the center of the screen in front of the monkey, the target stepped to an eccentric location and then back to the center. Each eccentric location and return step was repeated twice and then the eccentric location was shifted by one counterclockwise location, e.g., from an angle of 135° to an angle of 157.5°. After we had obtained preadaptation data under these conditions, we reduced the saccadic gain in both horizontal directions by the conventional adaptation paradigm and then repeated the sequence of oblique target steps.

Data analysis

To analyze the saccades, we digitized eye movement data online by sampling horizontal and vertical eye and target positions at 1 kHz. An analysis program then calculated the horizontal and vertical eye velocities and scrolled the target and eye position and eye velocity signals across a computer monitor. The program indicated the occurrence of the target step and marked the start and end of the horizontal and vertical components of each saccade according to an adjustable velocity criterion. On the basis of these markings, which could be modified by the investigator, a second program calculated the saccade metrics, e.g., saccade size, duration, and peak velocity, as well as several timing measures, e.g., saccade latency (reaction time) and time to peak velocity. For some of the analyses, commercial programs (Microsoft Excel, Wavemetrics IGOR and DataDesk) were used for further manipulations, such as sorting saccades according to size, direction, and sequential number in the experimental session.

Gain (G) was measured as the size of the saccade (E) divided by the size of the initial target step. Both before the adaptation began and after adaptation was complete, we measured the gain (Gpre and Gpost) of saccades to targets moving with simple steps without subsequent intrasaccadic backward jumps. The percentage of gain reduction was determined as

\[
\text{% Gain Reduction} = \frac{(G_{\text{post}} - G_{\text{pre}}))}{G_{\text{pre}}}
\]

Because we considered only target steps of 10°, this expression reduced to

\[
\text{% Gain Reduction} = \frac{(E_{\text{post}} - E_{\text{pre}}))}{E_{\text{pre}}}
\]

To assess the percentage of gain transfer from horizontal saccades adapted by the conventional paradigm to either the horizontal saccades elicited in the double-step virgin territory paradigm or...
the horizontal components of saccades elicited in the oblique-step
virgin territory paradigm, we first calculated the percentage of gain
reduction in each paradigm as discussed with respect to the Deubel
paradigm. Then we determined the percentage of gain transfer from
conventionally adapted saccades (% Gain Reduction\textsubscript{conventional}) to,
for example, the horizontal saccade elicited by the double-step
virgin territory paradigm (% Gain Reduction\textsubscript{conventional}) as

\[
\text{% Gain Transfer} = (\text{% Gain Reduction}_{\text{Deubel}})/\text{% Gain Reduction}_{\text{conventional}}
\]

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 and with
recommendations from the Institution of Laboratory Resources and
the American Association for Accreditation of Laboratory Care
International. The human experiments were conducted under
guidelines specified by the Human Subjects Review Committee at
the University of Washington.

\section*{RESULTS}

\textit{Deubel brief backstep paradigm}

Both monkeys and humans showed a reduction in saccadic
gain after being subjected to the Deubel paradigm even
though they made hardly any backward corrective saccades.
Representative responses early and late in adaptation to a
brief (117- to 150-ms) backward target movement are shown
in Fig. 1. Initially, this monkey (BW) and the four others
tested made normometric saccades or slightly hypometric
ones (Fig. 1A). As they experienced more and more trials in
which the target stepped backward, their saccades gradually
became consistently hypometric. By the end of the adapta-
tion, corrective saccades were predominantly in the forward
direction (Fig. 1B). The percentage of gain reduction for
the rightward saccades shown in Fig. 1 was 13.4%.

The Deubel paradigm produced different amounts of gain reduction in the same subject in the two adapted
directions (left and right) and on different days. The aver-
age gain reductions also varied considerably from subject
to subject. Such day-to-day and intersubject variations
also occur in monkeys when gain reduction is produced
by the conventional adaptation paradigm (Straube et al.
1997). The percentages of gain reduction produced by a
brief 30% backstep are summarized in Table 1. Gain
reduction ranged from 7.1 to 20.2% in monkey M and 7.5
to 16.1% in monkey TM over four experiments. Compara-
ble decreases in gain were obtained in the other three
monkeys in fewer experiments. Because there were no
consistent directional differences across monkeys, we
pooled the data for both directions for each monkey. The average (±SD) gain reduction over a total of 17 exper-
iments (2 directions each) in the five monkeys was 11.8 ±
1.9%. A comparable average gain reduction of 11.4% was
obtained in the two human subjects.

The gain reduction produced by the Deubel paradigm oc-
curred gradually. To document the course of adaptation, we
fitted the gains with exponential functions as we had done
previously for conventional adaptations (Straube et al.
1997). However, many fits of data obtained with the Deubel
paradigm were obviously inappropriate, as the data lacked
a clear asymptote. Therefore to compare the Deubel and
conventional adaptation data without making assumptions
about the form of the curve, we fitted both with a Lowess
smoothing function. This nonlinear fitting procedure in-
volves computing a regression line within a horizontal win-
dow around each y value and then assigning each data point
a weight inversely proportional to its distance from the fitted
line, thereby reducing the influence of outlying points. With
each iteration, these weights change, and the line converges
on the final fit (Cleveland 1979). Figure 2 shows the com-
plete course of gain changes both for the experiment of
Fig. 1 and for an experiment on the same monkey with
conventional saccadic adaptation. The rate or amount of gain
reduction was clearly less with the Deubel paradigm than
with conventional adaptation.

The difference in the courses of adaptation with the Deu-
bel and conventional paradigms is shown in Fig. 3, which
presents Lowess fits for representative experiments in both
directions for the four monkeys that had ≥750 adapted sac-
cades. To compare the maximum rate of gain change (which
occurs at the start of adaptation) in the two types of adapta-
tion, we determined the change in gain over the first 200
saccades of all five monkeys. In four of the five monkeys,
the initial rate of gain change was lower for the Deubel
adaptation than for the conventional adaptation. The ratio of
Deubel to conventional adaptation across 10 experiments (5
monkeys, 2 directions) had a median of 0.67 (mean, 0.59).
If, instead of treating each experiment separately, we average
across all Deubel adaptations, the average gain change over
the first 200 saccades was 0.030 ± 0.015. For the conven-
tional adaptation, it was 0.071 ± 0.038, yielding a ratio of
0.42. It is evident from the data in Fig. 3 that in the Deubel
experiments, as in the conventional adaptation experiments,
gain changes accumulated gradually rather than suddenly,
suggesting that true saccadic gain adaptation was occurring.
A sudden gain change in the Deubel experiments would have
suggested an entirely different mechanism, such as a change
in targeting strategy.

The gradual decrease in gain produced by the Deubel
paradigm occurred even though there were hardly any
backward saccades. For example, in the experiment shown
in Fig. 2, the incidence of backward corrective saccades
(plotted as the stepped line) was only ∼1% (15 of the
1,301 saccades made during adaptation). Similarly few
backward saccades were elicited in the other Deubel ex-
periments. For the representative experiments shown in
Fig. 3, the other three monkeys had minimums of 720,
824, and 846 adapting saccades in each horizontal direc-
tion. The percentage of saccades followed by backward
corrective saccades in these three experiments ranged
from 0.4 to 2.6%, with an average of 1.2 ± 0.9%. Within
each experiment, there was no consistent tendency for the
direction with more backward saccades to be associated
with a greater gain reduction. In contrast to adaptation using
the Deubel paradigm, in which only 1.2% of initial
saccades were followed by a backward corrective saccade
(∼10 saccades overall), nearly every saccade in conven-
tional adaptation was followed by a backward corrective
saccade. Therefore, if adaptation were driven solely by
backward corrective saccades, one might expect the same
gain reduction of 11.8% that was seen over 846 saccades
in the Deubel paradigm to occur in the first 10 saccades
under conventional adaptation. This clearly did not happen
TABLE 1. Percentage decrease in saccadic gain after adaptation using the Deubel paradigm

<table>
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<td>9/18/96</td>
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<td>R</td>
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</table>

Values are means ± SD; SD of the grand average of monkey test subjects was 1.9. * Adapted in one direction only.

(see Fig. 2, Conventional Adaptation). Furthermore, if adaptation was driven solely by backward corrective saccades, one might expect no further Deubel adaptation beyond saccade 800 in Fig. 2, after which there were no backward corrective saccades at all. Adaptation, however, continued.

In the four experiments in the two human subjects, the number of backward corrective saccades ranged from 5 to 30. As in the monkeys, there was no relation between the number of backward corrective saccades and the magnitude of the gain change. Although some studies of conventional saccadic adaptation in humans have demonstrated significant gain change with as few saccades (McLaughlin 1967; Miller et al. 1981), the saccade target in those studies jumped between the same locations from trial to trial. When the target location was varied, as it was in our experiments, substantially more trials were required (Albano and King 1989; Miller et al. 1981). Therefore it again seems unlikely that these few backward corrective saccades were driving the gain reduction. Why the Deubel paradigm is less effective than the conventional adaptation paradigm is a question that will be addressed in the DISCUSSION.

Taken together, these data suggest that the primary error signal driving saccadic adaptation is not derived from the metrics of the corrective saccades. Instead, the signal that drives adaptation would seem to be a visual error, a topic that will be considered further in the DISCUSSION. Regardless of the nature of the error signal, the question remains as to whether the adaptation itself arises from a warping of the visual map, which then commands a smaller saccade (a...
Fig. 4A. Before adaptation, horizontal saccades to targets that stepped only horizontally (□ on the y = 0 line) were roughly comparable in size, on average, to the horizontal saccades that were part of two-saccade responses to targets that jumped first vertically and then horizontally. After several hundred trials of conventional adaptation in the horizontal direction, saccades to targets stepping horizontally to the left were reduced in amplitude by 12.7% and those to the right by 16.8%. Horizontal saccades that were part of double-step responses to nonadapted target locations showed comparable reductions in amplitude: for targets appearing on the left either 7.5° above or below the adapted target location, saccades were reduced by 18.8% (if above) or 12% (if below); for targets to the right, saccades were reduced by 20.8% (if above) and 15.2% (if below).

Therefore, there was a >90% transfer of the gain reduction produced by adapting horizontal saccades to horizontal saccades made toward targets that were some distance from the retinal site at which the adaptation trials had occurred.

Similar results were obtained in more extensive experiments on two other monkeys (Table 2). As with most parameters of saccadic adaptation, however, there was considerable animal-to-animal and day-to-day variation in the magnitude of both the gain reduction and the gain transfer to new target locations. For example, in the four experiments on monkey BW, the percentage of transfer consistently was greater to rightward saccades than to leftward ones, and for any particular target locus, e.g., down/right, the percentage of transfer varied considerably from day to day. In contrast, monkey K showed relatively little variability from day to day and in different directions in its two experiments. Despite these differences, the average percentages of gain transfer for these two monkeys were within 7% across all directions, yielding a grand mean of 82%.

Conventional adaptation tested by single oblique steps to virgin territory

The substantial transfer of gain reduction demonstrated in the preceding section argues against the hypothesis that sensory adaptation (or is a direct alteration of premotor signals (a motor adaptation). We explored these alternatives in two different experiments in which we produced saccadic gain reduction by stepping targets on one part of the retina and then tested whether that gain reduction transferred to other parts of the retina (i.e., virgin territories) that had not experienced the adapting stimuli.

Conventional adaptation tested by double-steps in virgin territory

We next tested whether the adaptation is specific to a particular locus in the visual field (as would be expected if the plasticity involved changes in the static map of the visual field) or to a particular direction and amplitude of saccade (as would be expected if the adaptation was motoric). After using the conventional adaptation paradigm to reduce the gain of horizontal saccades, we measured the amount of this gain reduction that transferred to horizontal saccades toward targets at retinal loci that had not seen the target during the adaptation. We did this by eliciting first a vertical and then a horizontal saccade as detailed in the METHODS and schematized in Fig. 4. Data from a representative experiment on monkey M are shown in Fig. 4B.
in the horizontal direction reduced the gain of horizontal saccades by an average of 16.3% to the right and 17.0% to the left. Saccades to oblique targets, with either an upward or downward component, showed average gain reductions of ~7.4% for targets appearing to the right and ~9.9% for targets appearing to the left. Therefore the percentage of gain transfer from horizontal adapted saccades to the horizontal component of 45° oblique saccades was 45% for those with rightward components and 58% for those with leftward components (Table 2). This average of ~50% transfer to the single oblique-step paradigm, compared with >90% transfer in the double-step paradigm in the same monkey (Fig. 4A, Table 2), indicates that visual field remapping could explain only part of the double-step data.

Similar conclusions can be drawn from the more extensive experiments on the other two monkeys (Table 2). Again, the oblique-step data varied somewhat according to target locus; the data also varied from experiment to experiment. Nevertheless for both monkeys, the average percentage of transfer was always less in the oblique-step paradigm than in the double-step paradigm for targets in all four quadrants (Fig. 5). The difference in percentage of transfer ranged from 23 to 55% in monkey BW and from 38 to 48% in monkey K. Across all three monkeys and for all directions, the average transfer of gain to double-step targets was roughly twice as great (92%) as that to oblique-step targets (44%). This difference is statistically significant by analysis of variance ($F = 17.1, df = 1.12, P = 0.01$). It is unlikely that this difference is due to different amounts of horizontal adaptation training because the average number of trials across the two types of experiments was within 5% (double-step experiments, 2,110 trials, averaged over 12 experiments in 2 monkeys; oblique experiments, 2,236 trials, averaged over 17 experiments in 2 monkeys).

Finally, as a further check that these results were not due to differences in the training that preceded the experiments using single oblique steps and double steps, we measured the transfer during those double-step trials in which erroneous single oblique saccades were made directly to the target. In one experiment with monkey BW, transfer in the four
FIG. 4. Transfer of conventional gain adaptation to saccades made to targets in 4 non-adapted virgin territories. Conventional adaptation consisted of 30% backward jumps during saccades to 10 and 7° horizontal target steps. Gain reductions in right- and leftward saccades produced by conventional adaptation are shown on the abscissa in both A and B. Panels to the right illustrate the 2 experimental conditions. In A, while the animal was looking straight ahead, the target stepped 1st vertically by 7.5° (1) then horizontally by 10° (2). As the eye made a vertical saccade, the target was extinguished (3) and, in complete darkness, the eye completed the vertical saccade and then executed a horizontal saccade (4). The horizontal saccade of this double-step, memory-guided pair has the same direction and amplitude as the saccades made during adaptation. In B, the target went directly to the same virgin territory loci as in A (1). As the eye saccaded to the target, it went out (2) and the saccade was completed in the dark. The horizontal component of this oblique saccade shows less reduction than does the horizontal saccades to double steps in A.

The target always remained on, unlike the case in the previous experiments. In all cases, gain reduction was maximal in the adapted horizontal direction and fell off as an oblique saccade assumed greater vertical components (Fig. 6). The average gain reduction in the adapted horizontal direction across experiments was 18.5 ± 4.6%. The average gain reductions for the horizontal components of oblique saccades were 7.8 ± 2.6% for those directed 45° upward and 8.1 ± 2.6% for those directed 45° downward. Therefore, the gain transfer from the adapted direction was 43%, which compares well with the 44% transfer to the oblique control saccades in the double-step experiments. The lack of 100% transfer argues that the adaptation occurs before the saccadic command is sorted into muscle coordinates. Were that not the case, one would expect the degree of horizontal adaptation to be the same, regardless of whether or not a vertical component was present.

DISCUSSION

The experiments described here yielded two principal results. First, saccadic gain was decreased by adaptation even
Oblique loci were reached by two saccades in the double step task and a single saccade in the oblique step task. In the oblique step task, transfer was determined from the horizontal component of the oblique saccade. * Vertical component of 7.5°. ‡ Vertical component of 10°.

Our interpretation of the first result is that saccadic gain is reduced even when the visual error signal is present only briefly. Furthermore, gain reduction occurs whether corrective saccades are in the same direction as the primary saccade (as in adaptation using the Deubel brief backstep paradigm) or in the opposite direction (as in conventional adaptation), implying that corrective saccades do not provide an essential error signal for adaptation.

We presume that saccadic gain adaptation serves to keep the gain near unity. An alternative interpretation holds that the function of saccadic gain adaptation is not related to saccadic accuracy but instead serves to minimize the total time spent in saccades (Becker 1989; Harris 1995). This view is partly based on the fact that most normal saccades are hypometric (Becker and Fuchs 1969; Harris 1995; Henson 1978) and that this hypometria is actively maintained in the face of experimental perturbations (Henson 1978). According to this view, backward corrective saccades are more undesirable than forward ones because the eye must retrace the course just traveled. A simple way to minimize backward corrective saccades might be for their presence to signal that the saccadic gain is too high and cause the gain to decrease by more than forward corrective saccades caused it to increase.

Our results using the Deubel paradigm, however, are not consistent with this interpretation or with any that posits that the direction of the corrective saccades provides the only
error signal driving saccade adaptation. After a few hundred saccades, essentially all corrective saccades are forward, a condition that should lead to a gain increase instead of the gain decrease that actually occurred. Furthermore, after saccade 800 in Fig. 2 (Deubel Adaptation), no further backward saccades occurred and yet gain reduction continued. We infer that the direction of corrective saccades is not essential for saccadic adaptation. We cannot exclude the possibility, however, that the gain is adjusted not by the direction of the corrective saccades themselves, but by the direction of the corrective saccades that were programmed but then canceled when the target returned to its original location.

We infer from the adaptation produced with the Deubel paradigm that it is the presence of the target spot off the fovea after a saccade that serves as the error signal for adaptation. Why then is the Deubel paradigm less effective than conventional adaptation in producing saccadic gain adaptation (Fig. 3)? We will consider four possible explanations. First, the Deubel paradigm might be less effective because the direction of corrective saccades does provide an error signal for saccade adaptation, but it is simply not as effective as the visual one.

Second, this difference in efficacy of adaptation may be attributable to differences in the relation of the target and fovea in the period after each saccade. In conventional adaptation, after a saccade the target remains on one side of the fovea until a corrective saccade occurs. In that situation, the error signal is constant in magnitude and direction. In the Deubel paradigm, on the other hand, once the gain has declined a bit, the target appears on one side of the fovea after the initial saccade and then shortly after jumps to the other side before the corrective saccade (Fig. 1B). Thus in this situation the error signal switches both in magnitude and in direction. Because the latency to the corrective saccade in the Deubel paradigm was considerably greater than the latency to the primary saccade (an average of 102 ms longer in representative experiments from 4 monkeys), the target was beyond the fovea during most of time between the backstep and the corrective saccade (an average of 64% of the time in the same 4 monkeys). The fact that the Deubel paradigm produces adaptation at all probably indicates that the adaptation mechanism is most sensitive to the position error immediately after the saccade. However, the lower efficiency of the Deubel paradigm in producing gain reductions might suggest that the position error still can affect adaptation even several hundred milliseconds after the initial saccade, i.e., after the target returns from its brief backstep. This interpretation is supported by experiments showing that gain adaptation still occurs even if the target is turned off when the saccade is made and then reilluminated at a backstepped location ≈400 ms after the saccade (Fujita et al. 1996).

Third, if adaptation also affects the gain of corrective saccades, the Deubel paradigm imposes conflicting demands on the adaptation mechanism because the position error after the first saccade is backward (Fig. 1B), encouraging a gain decrease, but it is forward after the corrective saccade, encouraging a gain increase. In contrast, for conventional backward (gain reduction) adaptation, the position error after both the primary and corrective saccades is backward and therefore always promotes a gain decrease. The possible deleterious effect of the corrective saccade in the Deubel paradigm would be somewhat mitigated by the size difference between the two types of saccades; in our experiments, the corrective saccades were <3° compared with 10° for the primary saccades.

Fourth, one could argue that conventional adaptation is more successful because subjects attend to the target in preparation for making a saccade to it. In the Deubel paradigm, the target may be less salient during the backstep because attention or motor preparation is directed forward to where the target is about to appear and to where the impending corrective saccade will be made, rather than backward to the target’s temporary position. If this suggestion has merit, it further emphasizes the importance of the visual error signal in adaptation because saccadic gain is nonetheless decreased by this paradigm.

Thus we do not claim that our experiments eliminate the possibility that a motor error signal, such as the direction of the corrective saccade, may influence saccadic adaptation.
We argue only that such an error signal is not necessary for saccadic adaptation.

**Saccadic gain adaptation is motor not visual**

Our second principal result was that conventional adaptation of horizontal saccades was substantially transferred to horizontal saccades to novel target locations. We interpret this result as evidence that the adaptation was principally a motor adaptation specific to horizontal saccades rather than a consequence of a remapping of visual space. These results are consistent with recordings from neurons in the intermediate and deep layers of the monkey superior colliculus. These neurons show the same saccade-related activity to particular targets before and after adaptation, as though the adaptation changes occurred downstream from the recording sites (de Graaf and van Opstal 1997).

If static visual remapping were elicited by our adaptation paradigm, one could imagine it taking several possible forms. First, visual space could be remapped locally, so that if saccades to a point 10° left of the fovea consistently land beyond the target, that small region of the map might be reassigned to represent 8°; thus a target at 10° left would be perceived as being at 8° left. Our results have shown that this sort of remapping does not account for saccadic adaptation, because there is nearly complete gain transfer to retinal locations above or below the adapted location. Alternatively, conventional adaptation could provoke a more extensive warping of the visual map, so that a large area around the local adapted region is remapped. Were this the case, it would not be surprising if gain adaptation transferred to nearby regions. Our results also argue against this sort of visual remapping because conventional adaptation produced only ~44% transfer to a location in virgin territory if it was reached by oblique saccades, whereas horizontal saccades to the same location showed ~92% transfer (Fig. 4). Finally, one could argue that a visual map is altered, but instead of being the primary perceptual map, it is a visual map dedicated only to specific saccade tasks. This possibility would require the brain to maintain one map of visual space solely for use in the targeting of horizontal saccades, and other maps for other saccade directions.

These arguments against static visual remapping would not apply to dynamic maps updated after every saccade and before the programming of the next saccade. In such a map, the final target in our double-step virgin territory experiment would not have appeared in a novel region of the map when the horizontal saccade was being programmed because once the vertical saccade had taken place, the target would be at 10° horizontal, that is, at the adapted location. A neural signal reflecting such remapping has been described in the lateral intraparietal area, the frontal eye fields, and the superior colliculus (Bracewell et al. 1996; Colby et al. 1996; Mazzoni et al. 1996; Umeno and Goldberg 1997; Walker et al. 1995). Our results in the virgin territory experiment are certainly consistent with such remapping, which we are inclined to view as being more motor than visual because it is so closely tied to impending saccades.

Because the transfer from conventional horizontal adaptation to the horizontal component of oblique saccades (~44%) was considerably less than that to a horizontal saccade to the same virgin territory (~92%), we conclude that adaptation is more specific to the direction of the saccade than to the location of the target. The lack of robust transfer to the oblique saccades, despite the fact that they had the same horizontal components as the adapting saccades, argues that adaptation occurs before the saccadic command signal has been sorted out into components for the different extracocular muscle pairs. The fact that there was some gain transfer to oblique saccades is not surprising because adaptation of saccades in one direction is known to show some generalization to nearby directions (Deubel 1987; Frens and van Opstal 1994). At angles of 45° from the adapted direction, Deubel (1987) found that humans showed about half as much transfer as we found, whereas Frens and van Opstal (1994) found much greater transfer than we found. We have no explanation for these disparate results.

We are not the first to look for sensory remapping associated with saccadic adaptation. Frens and van Opstal (1994) used a paradigm very similar to our paradigm of adapting horizontal saccades and testing the transfer to virgin territories, except that they used human subjects and tested larger saccades. They found, as we did, that if saccades of the same amplitude and direction as those made during adaptation (21° horizontal in their case) were made to a target distant from the original adaptation locus (19.5° in their case), the adaptation transfer was nearly complete (85%, if calculated in the way we have done), although there was a threefold range in transfer among their three subjects. In contrast, the transfer was much less for saccades that reached the adapted locus at an angle of 60° from the adapted horizontal direction.

**Sensory remapping and saccadic adaptation**

There is some uncertainty in the literature as to whether saccadic adaptation is associated with a generalized static visual remapping. Studies in humans indicate that after conventional saccadic adaptation there is good gain transfer to saccades elicited by other sensory modalities but poor transfer to somatic movements aimed at visual targets. If we assume that the same saccadic mechanism is used for saccades to visual and auditory targets and that the adaptive change is at the motoric level, it is not surprising that adaptation of saccades to visual targets transfers to auditory ones, as shown by Frens and van Opstal (1994), because no sensory remapping would be required. More provocative are other experiments that found poor transfer from adapted saccades to movements that pointed the finger or head at a visual target (de Graaf et al. 1995; Krolleer et al. 1996; McLaughlin et al. 1968), suggesting that the adaptation is not a manifestation of a generalized visual remapping. Alternatively, sensory remapping might occur, but it might be delayed relative to saccadic adaptation. For example, Moidell and Bedell (1988) found a small but consistent delay in the transfer of adaptation to psychophysical assessments of the distance of a target from the midline. Such a delayed sensory remapping would not have been detected in the studies by de Graaf et al. (1995), Kroeller et al. (1996), and McLaughlin et al. (1968) because the number of adapting trials was small (n = 90, 40–50, and 33, respectively). Such late sensory remappings of course would be the result rather than the cause of saccadic gain adaptation.

In summary, we are not arguing against the possibility of...
sensory remapping, but it does not seem to be required for saccadic adaptation. Indeed, such a sensory remapping may play an important role in visuomotor functions. Because saccadic gains are adjusted independently for different directions and distances, one can infer that there is an array of different gains. Such a deformable motoric map might be rather like the map of visual space. We speculate that these two maps might be kept in register by reciprocal sensory and motor recalibrations: the saccadic adaptation paradigms result in motor recalibrations, which in turn are used over a long time to recalibrate maps of visual space, as suggested by Maloney and Ahumada (1989). If one arranged to adapt rightward and downward saccades continuously for days or months, one might find that the metrics of visual space had altered and that this alteration might in turn affect saccades even to unadapted locations. Such alteration might even affect other modalities, such as finger-pointing.

In conclusion, we find that the simplest motoric error signal—the direction of corrective saccades—is not essential to guide saccadic adaptation, although the adaptation does reflect a motoric recalibration. This leaves the problem of what sort of visual error signal guides the saccadic adaptation, how it is distinguished from the myriad of similar targets in daily life, and at what level of the CNS this processing takes place.

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